



Volume 97 Part 1 June 2014

Centennial Issue

Celebrating 100 years of the Royal Society of Western Australia

Promoting Science in Western Australia
A review of some achievements



The Royal Society of Western Australia

To promote and foster science in Western Australia

Patron

Her Majesty the Queen

Vice-Patrons

His Excellency Mr Malcolm J McCusker, AC CVO QC Governor of Western Australia

Professor Lyn Beazley AO FTSE MA PhD

COUNCIL 2012-2014

President H Bekle
Immediate Past President P O'Brien
Vice-President W A Loneragan
Vice-President K Trinajstic
Hon Secretary L Milne
Hon Treasurer P O'Brien
Hon Editor P Armstrong

Councillors
A W R Bevan
L B Collins
C Florides
P Armstrong
H M Stace
S Toby

EDITORIAL BOARD 2012–2014

Editor-in-chief
P Armstrong, University of Western Australia
Associate Editors
H Bekle, Notre Dame University
A W R Bevan, Western Australian Museum
R Davis, Edith Cowan University
K A Haskard, Data Analysis Australia

D W Haig, University of Western Australia P Ladd, Murdoch University D Laird, Murdoch University H M Stace, Subiaco K Trinajstic, Curtin University M Van Keulen, Murdoch University K Wright, Curtin University

The Royal Society of Western Australia was founded in 1914. The Society promotes exchange among scientists from all fields in Western Australia through the publication of a journal, monthly meetings where interesting talks are presented by local or visiting scientists, and occasional symposia or excursions on topics of current importance. Members and guests are encouraged to attend meetings on the third Monday of every month (March–November) at 7 pm, Kings Park Board offices, Kings Park, West Perth, WA 6005, or as advertised, in the RSWA Proceedings, Diary of Events.

Individual membership subscriptions for the 2013/2014 financial year are \$85 for ordinary Members, \$45 for Student Members and \$45 for Associate Members. For Library, company and institution subscriptions see the Society's website http://www.rswa.org.au. Prices include GST. For membership forms, contact the Membership Secretary, PO Box 7026, Karawara, Western Australia 6152, or visit the website http://www.rswa.org.au.

The Journal of the Royal Society of Western Australia was first published in 1915 and was renamed WA Science—Journal of the Royal Society of Western Australia in its Centennial Year 2014. Its circulation exceeds 650 copies. Nearly 100 of these are distributed to institutions or societies elsewhere in Australia. A further 300 copies circulate to more than 40 countries. The Society also has over 350 personal members, most of whom are scientists working in Western Australia. The Journal is indexed and abstracted internationally.

Cover design: The images symbolise the diversity of sciences embraced by the Royal Society of Western Australia. Counter-clockwise from the top they are: Wolfe Creek Meteorite Crater; the world-famous stromatolites at Shark Bay; the numbat (Myrmecobius fascialus), Mangles' kangaroo paw (Anigozanthos manglesii) and Gogo fish (Mcnamaraspis kaprios), which are the faunal, floral and fossil emblems of Western Australia, respectively; a zircon grain (Western Australian rocks have yielded the oldest zircon dates in the world, up to 4.37 Ga); and the black swan (Cygnus atratus) that appears on the logos of the Royal Society and the Government of Western Australia.

CONTENTS

PREFACE	iii
HISTORY History and roles of the Royal Society of Western Australia A W R Bevan	. 1
ARCHAEOLOGY Maritime archaeology in Western Australia J N Green 1 4 DEC 2015	13
BIOLOGICAL SCIENCE Vegetation survey in Western Australia N Gibson	25
Progress and prospects for understanding evolution and diversity in the Southwest Australian flora K R Thiele & S M Prober	35
Phytophthora cinnamomi in Western Australia P A O'Brien & G E St J Hardy	47
Arachnida (Arthropoda: Chelicerata) of Western Australia: overview and prospects M S Harvey	5 <i>7</i>
Relicts, reproduction and reintroductions—a century of marsupial research in Western Australia N M Warburton	65
CHEMISTRY	
Chemical fingerprinting of gold using laser ablation–inductively coupled plasma–mass spectrometry (LA-ICP-MS) R J Watling, C J Scadding & C D May	87
EARTH SCIENCE	
Geochronology of the Archean of Western Australia: a historical perspective R T Pidgeon & M T D Wingate	97
Early Paleozoic colonisation of the land: evidence from the Tumblagooda Sandstone, Southern Carnarvon Basin, Western Australia K J McNamara	111
Devonian vertebrates from the Canning and Carnarvon Basins with an overview of Paleozoic vertebrates of Western Australia	
K Trinajstic, B Roelofs, C J Burrow, J A Long & S Turner Devonian Great Barrier Reef of the Canning Basin, Western Australia:	133
the evolution of our understanding P E Playford, R M Hocking & A E Cockbain	153
Recent mega-tsunamis in the Shark Bay, Pilbara, and Kimberley	133
areas of Western Australia P E Playford	173
Stromatolite research in the Shark Bay World Heritage Area L B Collins & R J Jahnert	189
Drought and flooding rains: Western Australian water resources	
at the start of the 21st Century D P Commander	221
Some Australian contributions to meteoritics from the 19th to the 21st Centuries A W R Bevan	227
MATHEMATICS	,
Advances in mathematics and statistics in Western Australia since 1960 A P Bassom, J Hopwood, J L Noakes, A G Pakes & C E Praeger	253
EDITOR'S NOTE	261



PREFACE

Promoting Science in Western Australia A review of some achievements

The year 2014 marks the one hundredth anniversary of the granting of the Royal Charter to the Royal Society of Western Australia (RSWA). There had been several forerunner societies to the RSWA—Western Australian Natural History Society, Mueller Botanic Society, West Australian Natural History Society with which is incorporated The Mueller Botanic Society, and Natural History and Science Society of Western Australia: indeed the Society published a centennial issue of the Journal in 1998 to mark the foundation of the Mueller Botanic Society in 1897 from which the RSWA eventually evolved. Nevertheless it is approporiate to also celebrate 100 years of promoting science in Western Australia under the Society's Royal Charter.

Now is also the time to look forward to the next hundred years of science in Western Australia. To this end Council has decided to change the name of the Journal to WA Science (while retaining the Journal of the Royal Society of Western Australia as a subtitle) to emphasise the Society's role as set out in its Constitution 'to promote and assist in the advancement of science'. This is the first issue of the Journal under its new title and cover and contains papers reviewing significant aspects of scientific research that have been undertaken in Western Australia. A glance at the contents shows the breadth of research covered in this issue: a perusal of the list of authors reveals that many are members of the Society, demonstrating the active involvement of the Society in WA Science.

Bevan, in the introductory *History and roles of the Royal Society of Western Australia*, outlines the history of the Society; its formation, Journal, insignia and scientific role. He also explains why in its Centennial year the Society's Journal is Vol 97!

The remaining papers are grouped under the major disciplines they represent.

Green's *Maritime archaeology in Western Australia* reviews the development of the legislation to protect the State's underwater cultural heritage, with Western Australia enacting the world's first underwater cultural heritage legislation in 1963. The author discusses the work of the Western Australian Museum on shipwrecks on the Western Australian coast from the early shipwreck of the Trial in 1622 to the more recent wrecks of HMAS Sydney and HSK Kormoran in 1941.

Under Biological Sciences there are three botanical and two zoological papers.

The three botanical papers cover a diversity of topics. In *Vegetation survey in Western Australia*, Gibson documents the work of Ludwig Diels, Charles Gardner and John Beard in producing increasingly more detailed biogeographical classifications and vegetation maps for Western Australia. The author examines what might be needed to continue this work at higher resolutions. Thiele & Prober's *Progress and prospects for understanding evolution and diversity in the Southwest Australian flora* reviews the remarkable flora of southwest Australia with its high species richness and endemism and compares it with the flora of southeast Australia, confirming that southwestern Australia has higher species richness but lower generic and family richness than southeastern Australia. Dieback disease is reviewed in *Phytophthora cinnamomi in Western Australia* by O'Brien & Hardy. The pathogen *Phytophthora cinnamomi* has a wide host range; many Western Australian species of native plants are susceptible, and a large number are threatened with extinction. The authors look at the mechanisms by which *P. cinnamomi* causes disease and also at possibilities for control of the pathogen.

The two zoological papers deal with invertebrates and vertebrates. In *Arachnida* (*Arthropoda*: *Chelicerata*) of *Western Australia*: overview and prospects Harvey provides a history of the study of arachnids (spiders, scorpions, ticks, mites and their relatives) in Western Australia. The fauna consists of at least 1400 named species and it is estimated that ~6000 species exist, the majority of which are currently undescribed. Warburton's *Relicts, reproduction and reintroductions—a century of marsupial research in Western Australia* reviews the quintessential Australian animals, that have attracted considerable interest from the scientific community, both at home and abroad under the headings: taxonomy and natural history ('relicts'); reproductive biology and physiology ('reproduction') and conservation ecology ('reintroductions').

The sole chemistry paper, Watling, Scadding & May's Chemical fingerprinting of gold using laser ablation—inductively coupled plasma—mass spectrometry (LA-ICP-MS), documents the development of a gold fingerprinting protocol, using laser ablation—inductively coupled plasma—mass spectrometry and overviews the application of the technology and highlights its use in specific cases of gold theft.

There are eight Earth Science contributions, again emphasising the diversity of research in this area of science. In *Geochronology of the Archean of Western Australia: a historical perspective* Pidgeon & Wingate present a brief overview of the role of isotopic dating in providing numerical measurements of the geological age of igneous and metamorphic events and resolving key questions on the evolution of the Pilbara and Yilgarn Cratons. They also highlight major achievements, including the identification of the oldest fragments of the Earth's crust in metasedimentary rocks of the Yilgarn Craton and the determination of the age of the world's oldest fossils in the Pilbara Craton.

Turning to younger rocks McNamara, in *Early Paleozoic colonisation of the land: evidence from the Tumblagooda Sandstone, Southern Carnarvon Basin, Western Australia* documents the great variety of trace fossils in the Tumblagooda Sandstonde, which he argues is of early to mid-Silurian in age. This nascent terrestrial fauna was dominated by arthropods. The presence of extensive dwelling burrows and terrestrial trackways in the *Scoyenia* ichnofacies may represents the earliest known freshwater/terrestrial ecosystem and supports the view that one of the major steps in evolution, the colonisation of land by animals, may have been from rivers, rather than directly from the sea.

Devonian rocks receive attention in two papers. In Devonian vertebrates from the Canning and Carnarvon Basins with an overview of Palaeozoic vertebrates of Western Australia, Trinajstic, Roelofs, Burrow, Long & Turner review recent work on the exceptionally well preserved Late Devonian fauna of the Gogo Formation that has revealed new information on bone growth, muscle attachments, the evolution of teeth and reproductive structures, and live birth in early vertebrates. This and work on Early Carboniferous faunas from the Canning, Carnaryon and Bonaparte Basins are providing information on faunal patterns and exchange of vertebrates through the Paleozoic, which is at odds with paleogeographic reconstructions based on paleomagnetic evidence. Playford, Hocking & Cockbain's Devonian Great Barrier Reef of the Canning Basin, Western Australia: the evolution of our understanding reviews the historical development of our understanding of the world famous Devonian reef complexes that are spectacularly exposed along the northern margin of the Canning Basin in Western Australia, and have become renowned as 'The Devonian Great Barrier Reef'. The geological literature on these rocks dates back to 1884; the first studies of the biostratigraphy were conducted during the 1940s and systematic mapping the reefs started in the late 1940s and early 1950s, and since then studies by many individuals and organisations have progressively increased knowledge of the stratigraphy and paleontology of these reef complexes culminating in 2009 with the publication of the Geological Survey of Western Australia's comprehensive bulletin on the geology of the reef complexes.

The Shark Bay region is discussed in two papers. Playford's Recent mega-tsunamis in the Shark Bay, Pilbara, and Kimberley areas of Western Australia describes the very large blocks of calcrete, some weighing more than 700 t, thought to have been the products of mega-tsunamis, that lie on flat karstified calcrete surfaces behind coastal cliffs in the Shark Bay area and on Barrow and Legendre Islands. Other mega-tsunami deposits are known from the Kimberley, where they include large blocks of Proterozoic siliceous sandstone and mafic igneous rocks. Oysters encrusting the boulders have been dated: two samples of oyster shells from Legendre Island, and seven from Barrow Island, have been radiocarbon dated as 2895 and 3777 years BP (Legendre Island) and 3498 to 5444 years BP (Barrow Island). The tsunamis that struck the Kimberley coast have not been dated but may be associated with seismic activity along the Sunda and Banda Arcs of Indonesia. The origins of mega-tsunamis that impacted on the coast from Shark Bay to the Pilbara are uncertain but it seems likely that they originated from large-scale slumping of sediment on the continental slope (possibly initiated by earthquakes) or local faulting. The world famous stromatolites are described by Collins & Jahnert in Stromatolite research in the Shark Bay World Heritage Area. Detailed mapping has revealed extensive subtidal microbial deposits occupying ~300 km² of the total Holocene 1400 km² area of Hamelin Pool. The microbial pavement covers 227 km² of the subtidal substrate, which together with columnar structures reveals a subtidal microbial habitat that occupies an area several times larger than the area of the intertidal deposits. Oldest dated stromatolite heads are 1915 14C years BP, and the overall system was deposited in two stages: the first between 2000 and 1200 and the last from 900 years BP to the present. Slow accretion rates vary from less than 0.1 to 0.5 mm/year. Evidence of shallowing-upward fabric sequences of microbial origin reflects relative falling sea levels during the late Holocene and is likely useful in ancient environmental interpretation.

Commander reviews the water resources of the State in *Drought and flooding rains: Western Australian water resources at the start of the 21st Century.* The drying climate of southwestern Western Australia has led to much reduced runoff and groundwater recharge, with consequent decline in groundwater levels affecting wetlands and groundwater-dependent ecosystems while desalination has replaced the failing surface water supplies from hills catchments. At the same time, the north and northwest of the State have an increasingly wet climate in the last decade. The challenge for the State is to optimise use of the existing water resources and make best use of the undeveloped surface and groundwater. With groundwater and surface water resources increasingly fully developed, the emphasis for the future will be on recycling and water-use efficiency.

The eighth paper in this section, *Some Australian contributions to meteoritics from the 19th to the 21st Centuries* by Bevan, documents some of the significant achievements that have been made in the study of meteorites in Australia. Meteorites are fundamental to our understanding of the origin and early evolution of the Solar System. Many have remained virtually unaltered for 4.56 Ga and represent some of the original materials from which the planets were constructed. From the 19th Century onwards contributions to the understanding of planetary materials have been made by Australian scientists in the fields of meteorite recovery, mineralogy, petrology and metallurgy of meteorites, meteorite classification, isotopic studies, geochronology, impact cratering and Solar System formation.

The final paper is in a discipline that has featured all too rarely in the Society's Journal. In *Advances in mathematics and statistics in Western Australia since 1960* Bassom, Hopwood, Noakes, Pakes & Praeger, review some of the key developments in mathematics and statistics over the last half-century concerning researchers either based in, or originating from, Western Australia. The authors describe the whole range of mathematical sciences from the work in the most abstract and theoretical aspects of pure mathematics through to the most applied area of statistics and provide an insight into the work of the mathematical community in Western Australia.

It remains for me to thank the authors, and reviewers, for the time and effort they have put into bringing this Centennial Issue to fruition. Nevertheless, it has not been possible to cover the whole spectrum of scientific endeavour in Western Australia, and some readers may feel that there are glaring omissions. We therefore invite those who think their field of science has been neglected to prepare and submit a review to the new Journal so that it can indeed continue to 'promote and assist' WA Science in all its aspects.

A E Cockbain Hon Editor: Centennial Issue June 2014



History and roles of the Royal Society of Western Australia

A W R BEVAN

Department of Earth and Planetary Sciences, Western Australian Museum, Locked Bag 49, Welshpool DC, WA 6986, Australia Alex.bevan@museum.wa.gov.au

The Royal Society of Western Australia (RSWA) was established on 10 March 1914 under Royal assent granted by King George V, and remains to the present day the only multi-disciplinary scientific society in the State. In the hundred years of its existence, the Society has published 10 volumes of the Journal and Proceedings of the RSWA and, following a name change, 87 volumes of the Journal of the RSWA, including many significant thematic issues. Due to printing difficulties, three volumes of the Journal were lost in the 1940–1950s. Since 1924, the Society has awarded 24 RSWA medals to scientists for outstanding contributions to science. The Society is the peak body for science in the State, and continues to be involved in many scientific issues of the day. In its Centenary year, this paper provides a history of the Society; its formation, Journal, insignia, and scientific roles.

KEYWORDS: awards, history, insignia, journal, library, management, roles, Royal Society of Western Australia, science.

INTRODUCTION

The Royal Society of London was founded in 1660 as 'a Colledge for the Promoting of Physico-Mathematicall Experimentall Learning'. Through the patronage of King Charles II, the 'Colledge' became the Royal Society. The name Royal Society first appears in print in 1661, and under a second Royal Charter in 1663 the Society is referred to as 'The Royal Society of London for Improving Natural Knowledge'. In the context of societies, the use of 'Royal' without further qualification is confined to multi-disciplinary scientific bodies sharing the same purview as the Royal Society for 'improving natural knowledge'. Other 'Royal' societies are further qualified and subject-specific, such as the Royal Zoological Society, the Royal College of Surgeons, the Royal Historical Society, and the Royal Astronomical Society. Following in the tradition of the first Royal Society, 'Royal Societies' were established in some of Britain's former colonies and many persist to the present day, like the Royal Societies of Canada, South Africa and New Zealand. Of the six state-based Royal Societies in Australia (the others being New South Wales, Tasmania, Victoria, South Australia, and Queensland), the Royal Society of Western Australia (RSWA) is the youngest. All of these societies follow in the tradition of the original Royal Society.

This year (2014), the RSWA celebrates its Centenary of establishment. However, the RSWA was born out of several pre-existing scientific societies, and their histories, along with the subsequent history of the RSWA, document the rise in interest and involvement in science in Western Australia. Several histories of the RSWA have been written. The earliest was an unpublished account written by W M Traylen in 1924. Later, a Presidential Address by C F H Jenkins gave a broad and detailed account of the Society's history to that date (Jenkins 1965). In addition, historical details of the Society were mentioned in a thesis submitted to the University of New

South Wales (Summers 1982). Most recently, P C Withers, a former President of the RSWA and Honorary Editor of the Journal of the RSWA, published an account of the 100 years (1897–1997) from the establishment of the forerunner 'Mueller Botanic Society' (Withers 1998). In the present paper a comprehensive history of the RSWA is presented in its true Centenary year.

EARLY YEARS

Western Australian Natural History Society 1891–1898

In 1891, the Western Australian Natural History Society was founded under the Presidency of Sir John Forrest KCMG, the first Premier of Western Australia. This coincided with the opening of the then Geological Museum (now Western Australian Museum) at the Old Gaol in Perth, an institution to which the subsequent RSWA would later become closely linked. The activities of the society appear to have concentrated on the preservation of lands, and one of its significant achievements was the establishment of a nature reserve of some several thousand acres between Pinjarra and Bannister. Unfortunately, this society did not flourish and by 1898 it had ceased to exist. However, its brief existence provided the impetus for the later establishment of natural history societies in the State.

Mueller Botanic Society

In 1897, a group of amateur botanists established the Mueller Botanical Society, again under the Presidency of Sir John Forrest KCMG. This society was named in honour of the renowned botanist Baron Ferdinand von Mueller. The first Chairman of the society was E J Bickford. The society was extremely active and, with the aid of a grant of £50 from the State Government, published a journal. The *Journal and Proceedings of the Mueller Botanic Society* ran for 11 issues (Volume 1) between 1899 and 1903 and contained some seminal botanical works.

By 1903, the Mueller Botanic Society had broadened its interests to other aspects of natural history. The name of the society was changed to 'The West Australian Natural History Society (with which is incorporated the Mueller Botanic Society)' and the first President of the expanded society was C R P Andrews MA, a botanist.

The newly named Journal of The West Australian Natural History Society, continued on from the former Journal and Proceedings of the Mueller Botanic Society publishing six parts of Volume II, beginning with No.1 in May 1904 and ending with No.VI in 1909.

Natural History and Science Society of Western Australia

The West Australian Natural History Society struggled during the early 1900s, and in 1907 several meetings of the society failed because of a lack of a quorum. To address the problem, the society's council suggested that monthly meetings be held when a paper was presented. A subcommittee was established to explore the possibility of establishing a Royal Society, or affiliating with the Royal Society of South Australia which had been established in 1880. In 1909, Andrew Gibb Maitland, then Government Geologist, and member of the former Mueller Botanic Society, suggested that, in recognition of sciences other than natural history and in an attempt to broaden the society's appeal, the name should be changed to the 'Western Australian Science and Natural History Society'. At the next general meeting of the Society, the name was formally changed with minor amendment to that suggested by Maitland to 'The Natural History and Science Society of Western Australia'.

The first President of the newly named society was Dr Frank Tratman. While a keen natural historian and member of the former Mueller Botanic Society, Tratman was a Doctor of Medicine, a member of the Medical Board of Western Australia and president of the Dental Board of the colony (Kimberly 1897).

Publication of papers continued as the *Journal of the Natural History and Science Society of Western Australia* with Volume III no.1 in 1910, and no.2 in 1911. Volume 'The Fourth' was published in 1912, and the series ended with Volume 'The Fifth' before the outbreak of World War I in 1914 (Withers 1998).

Royal Society of Western Australia

Once again Maitland was prominent in attempting to improve the standing of The Natural History and Science Society of Western Australia. In March 1913, Maitland gave notice that at the next meeting he would suggest that:

'the time has arrived for obtaining a Royal Charter for the Society and, if granted, altering the designation to the Royal Society of Western Australia'.

Maitland was absent at the next meeting in April and discussion was deferred to the May meeting. At the May meeting, noting the inauguration of 'The University' (of Western Australia), Council agreed that it was opportune to consider seeking a Royal Charter. Maitland resolved that:

'...the time has arrived for taking the necessary steps for

altering the designation to "The Royal Society of Western Australia", and for obtaining Royal assent thereto; and that the matter be left in the hands of the Council'.

A resolution was carried that:

'A sub-committee of Mr Maitland, Mr Grasby and the Secretary [Mr Browne] consider and report on the best manner of obtaining a Royal Charter'.

In June, the sub-committee recommended that a memorial be addressed to His Majesty King George V, and a letter to be written to His Excellency the Governor, Major-General Sir Harry Barron KCMG requesting that the memorial be forwarded to the King. At the Council Meeting of 10 June 1913 draft letters were tabled and a recommendation carried to proceed. On 27 June 1913, a memorial to the King along with a covering letter both signed by the President, C G Thorpe, and the Secretary, M A Browne, were submitted to the Governor.

Assent for the Royal Charter was received by the Society from His Majesty via the Governor in a letter dated 18th November 1913 and this was announced at the next meeting of the Society on 2nd December 1913.

[Transcription of a letter dated from Government House, Perth, on November 18th, 1913, and addressed to the Honorary Secretary of the Natural History and Science Society of Western Australia.]

Dear Sir

I am directed by His Excellency the Governor to inform you that His Majesty the King has been graciously pleased to accede to the application of the Natural History and Science Society of Western Australia for permission to assume the title "The Royal Society of Western Australia"

I have the honour to be,

Sir,

Your obedient Servant

(Signed) H. F. Wilkinson

Major,

Private Secretary

On 11 March 1914, an article (from which the following are extracts) was published in *The West Australian* newspaper reporting the formal assumption of the new title.

At the general meeting of the Natural History and Science Society, held last night [10th March 1914], the draft rules for the new Royal Society, as submitted by the Council, were discussed in detail, amended, and on the motion of the President (Professor Dakin) adopted. Professor Ross then secured a vote of thanks to the three members of the subcommittee, viz., Professors Dakin and Woolnough, and Mr Maitland, to whom the onerous duty of compiling the rules had fallen.

On the motion of Mr. M. A. Browne, it was resolved "That this Society be henceforth called 'The Royal Society of Western Australia', and that its management be vested in the present council until the election of the new council in July." Effect is thus given to the change of title for which the permission of His Majesty the King was received last November. The Royal Society, properly so called, will therefore hold its first meeting in April.

That the notice was so rapidly transmitted to the newspaper (the night before publication) was due to the Society holding its meetings in the building of *The West Australian* newspaper (Summers 1982). There remained the administrative details for the complete transition of membership from the Natural History and Science Society, to the Royal Society of Western Australia. *The West Australian* reported:

A motion by Mr. E. S. Simpson provides for the immediate transference of membership from the old to the new Society, such membership to remain in force till the annual meeting in July next. Two resolutions of importance both to present members and those wishing to join the Society, were proposed by Professor Ross and carried. They are worded as follows:—(1.) "That payment of the subscription of half a guinea for the year 1913-14 by members of the Natural History and Science Society, exempt them from any further contributions to the Royal Society of Western Australia until July 1, 1914." (2.) "That all members elected to the Royal Society of Western Australia between this date and July 1, 1914 shall pay only one annual subscription for the period to June 30, 1915, provided the sum be paid before June 30, 1914."

Thus the Royal Society of Western Australia was established under a new constitution adopted on 10 March 1914. A petition to His Majesty George V to act as Patron of the Society was granted via a letter from Government House, Perth, dated 11 March 1914 and noted in the Minutes of the Society at its meeting of 21 April 1914. At the same meeting, His Excellency the Governor, Sir Harry Barron KCMG, was unanimously elected Vice-Patron of the Society. Over the last 100 years the Society has continued to enjoy Royal Patronage by King Edward VIII and King George VI in 1936, and by George VI's successor, Queen Elizabeth II in 1952, and the Vice-Royal patronage of successive Governors of the State of Western Australia. In 2007 Council appointed Professor Lyn Beazley AO FTSE, Chief Scientist of Western Australia, as an additional Vice-Patron of the Society.

Incorporation

Recognising the legal and operational benefits of being a corporate body, at its meeting on 8 June 1936 the RSWA resolved to seek incorporation. To this end, the Society engaged the assistance of John Nicholson MLC and the legal firm of Nicholson & Nicholson. Mr W E Shelton, one of the Society's secretaries, was nominated as Trustee on 13 October 1936 to enable incorporation to proceed under an amended Constitution. In due course a certificate of incorporation was obtained and presented at the meeting of the Society on 7 July 1937.

JOURNAL AND PROCEEDINGS OF THE RSWA

Breaking with the previous practice of a continuous volume run throughout society name changes, the RSWA published Volume I of the new Journal for the year 1914–1915 that was printed in 1916 (priced at five shillings) (Figure 1). As an example of the truly multi-disciplinary nature of the RSWA, the first paper in Volume 1 is a mathematical contribution by one of the then Editors of the Journal, and former Secretary, Maurice A Browne

entitled: The approximate summation of series, in which each term is a function of the corresponding term of an arithmetical progression (Browne 1914).

The combined Journal and Proceedings of the Royal Society of Western Australia was eventually divided at Volume XI into the Journal of the Royal Society of Western Australia and the Proceedings of the Royal Society of Western Australia. The Proceedings was then, and is now, essentially the 'newsletter' of the Society containing at various times, notices of meetings, annual reports, financial statements, lists of members and announcements of new members, summaries of meetings, abstracts of monthly talks, and other items of interest to the membership.

As part of the normal Journal run, many issues have been published that are devoted to special thematic subjects, often resulting from topical Symposia. The first thematic issue is a compilation of papers devoted to research in the southwest of Western Australia (McComb 1973) to mark the occasion of the 45th Congress of ANZAAS held in Perth during April 1973. This was followed by an issue devoted to research on Rottnest Island (Bradshaw 1983). The most recent is a volume that arose out of a Symposium held jointly with the Western Australian Marine Science Institute on Kimberley marine and coastal science (Brocx & Meney 2011). Others include a Symposium on the Leeuwin current (Meney & Brocx 2009) and a Symposium on evolutionary biology (Meney & Brocx 2009)

While the Journal has enjoyed a run for 100 years, this year marks the publication of Volume 97. The discrepancy arises from a publication gap of two years between volumes 35 and 36 (1948–1949 and 1952) during which time the Society was negotiating with the Government regarding the printing of the Journal by the Government Printer on a new basis and, subsequently, from the serious setback caused by power restrictions, and a coal strike (Annual Report of the RSWA, 30 June 1949; P C Withers pers. comm. 2013). A further year was lost between volumes 39 and 41 (the period 1955–1958), again the result of printing difficulties. Since that time, no further years have been lost.

With the closure of the Government Print in the early 1990s, the Society had to find a new printer and this was provided by the Publications Department of the Western Australian Museum. To compensate for the loss of the subsidised printing provided by the Government Print, the State Government first through the Library of Western Australia, and then through the Department of Culture and the Arts, provided the Society with an annual printing subsidy of \$17 600 (including GST). This enables the Society to maintain the quality of the Journal and distribute copies to Government Departments.

Since 1992, the Journal has had only three Honorary Editors, P C Withers (President 1998–2000), K Meney (assisted by M Brocx) and, most recently, A E Cockbain (since 2012). However, it should be noted that Dr Cockbain (President 1982–1983) also acted as Editor for the period 1976–1982. Following the appointment of Dr Cockbain in 2012, an Editorial Board was instituted with several Associate Editors drawn from Council and the wider membership.

Journal and Proceedings

The Royal Society of Western Australia

PATRON: H.M. THE KING.

Volume I. 1914 - 1915.



Published August, 1915.

The Authors of Papers are alone responsible for the statements made and the opinions expressed therein.

Price: Five Shillings.

PERTH:
BY AUTHORITY: FRED. WM. SIMPSON, GOVERNMENT PRINTER.

1916.

Figure 1 Cover page of Volume 1 (1914–1915) of the Journal and Proceedings of the Royal Society of Western Australia.

CREST, MEDALS, SEAL AND EMBLEMS

The Crest of the RSWA, sometimes referred to as the 'medallion', was designed in 1915 for use on the Society's publications and letterhead, and first appeared in Volume I of the Journal (printed in 1916) (Figure 1). Subsequently, following incorporation in 1937, the Crest was modified to signify this. In addition, a 'common seal' to be used as an official stamp on documents was purchased from Shannon's Engraving & Stamp Co for 17s 8d (Withers 1998). The Crest was further revised and redesigned in 1997, and remains unchanged to the present day (Figure 2).

In 1924, the medal of the RSWA was inaugurated to mark the centenary of the birth of Lord Kelvin (26 June 1824). The medal (Figure 3) was instituted as an award for outstanding work in science, and it was to be known

as the Royal Society's Medal or, more formally, the Medal of the Royal Society of Western Australia. Because the medal bears the image of Lord Kelvin on its obverse side it has sometimes been referred to incorrectly as the 'Kelvin Medal' (Withers 1998). Professor A D Ross, as President in 1924, loaned his 'Kelvin Medal' that had been awarded to him by Glasgow University to make the die for the Medal of the RSWA. Professor Ross stipulated that the name 'Kelvin Medal' should not be used by the RSWA for its new medal.

The medal was designed by Miss Enid Isabel Allum for which she received an honorarium of five guineas. Miss Allum was a member of the Society, Treasurer from 1922 to 1927, and a member of the Social Committee. Through the Royal Mint in Perth, Messrs Stokes & Co. of Melbourne were commissioned to make the die for the



Figure 2 Current Crest of the Royal Society of Western Australia.

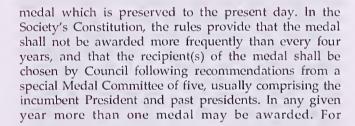




Figure 3 The Medal of the Royal Society of Western Australia.

example, in 1979 there were three recipients of the medal; Professor R. M. Berndt (President 1952–1953 and 1972–1973), Emeritus Professor B J Grieve (President 1970–1971), and Dr D L Serventy (Vice-President 1946–1949). In all 24 medals have been awarded (Table 1).

The first three medals were struck in gold, and all subsequent medals have been struck in silver. The first medal was awarded in 1924 to Dr William J Hancock

Table 1 Recipients of the Medal of the Royal Society of Western Australia

1924	Dr W J Hancock	Radiography; medical application of X-rays.
1929	Dr E S Simpson	Mineralogy and geology of WA.
1933	Mr W M Carne	Plant pathology; the bitter pill of apples.
1937	Mr A G Maitland	Pilbara survey and artesian water supplies.
1941	Professor E de C Clarke	Geology of WA.
1945	Mr L Glauert	Natural sciences.
1949	Mr C A Gardner	Botany, the flora of WA.
1955	Dr H W Bennetts	Vetinary science; live stock diseases.
1959	Professor E J Underwood	Animal nutrition and husbandry.
1966	Mr C F H Jenkins	Agricultural entomology and natural history.
1970	Professor R T Prider	Geology, petrology and mineralogy.
1979	Professor R M Berndt	Anthropology; aboriginal studies.
1979	Emeritus Professor B J Grieve	Botany; ecophysiology and the flora of WA.
1979	Dr D L Serventy	Zoology; ornithology and nature conservation.
1983	Dr J S Beard	Botany; vegetation classification and mapping.
1986	Professor C A Parker	Soil biology.
1993	Professor J R De Lacter	Geophysics and geochronology.
1995	Emeritus Professor A R Main	Zoology; ecology and nature conservation.
1997	Professor E P Hodgkin	Estuarine studies.
1997	Professor A J McComb	Plant growth and ecology.
2001	Dr P E Playford	Geology and history of discovery in WA
2005	Professor D I Groves	Economic geology and mineralogy.
2005	Dr K J McNamara	Palaeontology and evolutionary palaeobiology.
2010	Emeritus Professor S D Bradshaw	Ecophysiology; wildlife conservation.



Figure 4 William J Hancock (President 1918–1919), first recipient of the Medal of the RSWA in 1924.

(President 1918–1919) (Figure 4), Government Electrical Engineer and Honorary Medical Radiographer at Perth Hospital, for his pioneering studies in radiography and the medical application of X-rays. The second gold medal was awarded in 1929 to Dr E S Simpson for outstanding contributions to the scientific knowledge of the mineralogy and geology of Western Australia (Figure 5a, b).

The creation of Royal Society Top Student Science Medals for Perth's four public universities was discussed by Council in March 1997. In 1998 the RSWA inaugurated Student Medals to be awarded every year at its Annual General Meeting to those science students from each of Perth's universities nominated by them as the most outstanding in Natural and Earth Sciences. The obverse of the medal is the crest of the RSWA. Initially, medals were awarded to students from the University of Western Australia, Curtin University, Murdoch University and Edith Cowan University. The University of Notre Dame was included later. Student Medals were first awarded at the Society's Annual General Meeting on 20 July 1998.

In 2008, Council resolved to honour the life of Doug Clarke (Murdoch University) by initiating 'The Doug Clarke Education Advocacy Award Medal' of the Society. This award recognises the outstanding contribution to science education made by Doug Clarke. Clarke performed hundreds of chemistry shows at schools and regularly appeared on television. He inspired thousands





Figure 5 (a) Edward S Simpson, second recipient of the Medal of the RSWA in 1929. (b) Inscription on the Medal presented to Simpson.



Figure 6 The Doug Clarke Education Advocacy Award Medal of the RSWA.

of school children in the wonders of science, and assisted undergraduates and postgraduates. Three medals are awarded quadrennially for University Teaching Staff, a Secondary School Teacher, and a Primary School Teacher. The medal has Doug Clarke's image in relief on the obverse side (Figure 6), and the RSWA Crest on the reverse side. The inaugural award was presented to Doug Clarke at the Annual General Meeting of the Society in 2008.

Through an open competition of the membership, an emblem to appear on the front cover of the Journal was commissioned by Council. The winning design, by Jan Taylor, first appeared on Volume 75 (part 2) in 1992. The original emblem depicted one of the State's faunal emblems, the numbat (Myrmecobius fasciatus), and the floral emblem, the red and green kangaroo paw (Anigozanthos manglesii), together with a stylised illustration of stromatolites from Hamelin Pool. Later, an illustration of a reconstruction of the State's fossil emblem (proclaimed on 5 December 1995) a Gogo fish Menamaraspis kaprios (named for K J McNamara, RSWA Vice-President 1989-1991, President 1991-1992) was added. The State's other faunal emblem, the black swan (Cygnus atratus), appears on the Society's Crest together with the Latin pun 'Cygnis Insignis' (Noted for Swans).

MEMBERSHIP

The first published list of members of the RSWA in Volume I of the Journal showed 7 Honorary Members, 51 Ordinary Members and 27 Associate Members, a total of 85 members. This was a healthy number considering that World War I was at its height, and that some members were on active military service. The membership included many of the eminent scientists of the time in Perth and stalwarts of the RSWA and its forerunner societies, including; W J Dakin DSc, FLS, FZS, Professor of Biology at the University of Western Australia

(President 1913-1915); A G Maitland FGS, Government Geologist at the Geological Survey of Western Australia (Vice-President 1913-1915 and President 1915-1916 and 1924–1927); E S Simpson BE, BSc, DSc, FCS, Government Assayer, Geological Survey of Western Australia (Vice-President 1913-1914, 1918-1920, 1936-1938 and President 1920-1921, 1938-1939); A D Ross, MÄ, DSc, FRSE, FRAS, Professor of Physics and Mathematics at the University of Western Australia (Vice-President 1914-1916, 1939-1940 and President 1916-1917, 1923-1924, 1940-1941); and W B Alexander BA, MA, Keeper of Biology at the Western Australian Museum. The ordinary membership also included the Most Reverend C O L Riley, DD, Archbishop of Perth a keen natural historian, and President of the former West Australian Natural History Society (1906–1907). Among the Honorary Members was the Right Honorable Sir John Forrest GCMG, PC, FRGS, who by then had been elected to the Federal Parliament in Melbourne.

By July 1916 the total membership had increased to 96, including two new categories, Corresponding Members, and the Society's first Student Member, S K Montgomery. From an initial interest in science and involvement with the RSWA, Stephen King Montgomery BA(Hons), BSc(Hons), MB, BS(Lond), MD(Lond), DR (Edin) (1895-1950) went on to achieve scientific eminence. Having graduated from the University of Western Australia with honours degrees (BA and BSc in Zoology), in 1920 he entered University College Hospital, London, as a medical student. In 1930 he branched out into Radiology (Leftwich 1950). As well as a medical practitioner, Montgomery was a carcinologist of international repute. In 1931 his monograph on Crustacea Brachyura of the Percy Slade Trust Expedition to the Abrolhos Islands, together with Crabs of Western Australia, was published in the Proceedings of the Linnean Society. Montgomery published only one paper in the Journal & Proceedings of the Royal Society of Western Australia on Some Hymenosomidae from the Swan River (Montgomery 1919).

The membership grew steadily through the early part of the 20th Century. By June 1924 the Society had 253 members, and in that year alone it had gained 93 Ordinary and 29 Associate Members. While neither the RSWA nor its forerunner societies ever required that members had special academic qualifications, the membership at that time included many working scientists, the Chief Justice and other members of the judiciary, 4 politicians, 7 university professors, 13 medical practitioners, the Director of Education, the Director of Agriculture, and many prominent businessmen of the day.

By 1965 the membership had stabilised at 246. While remaining buoyant, the Society's membership had grown very little from its peak in 1923–1924. Jenkins (1965) noted that a similar change had occurred in other States' Royal Societies and this was attributed to the impingement of specialist societies on the membership. This remains true to the present day.

During the 1990s the Council of the Society took a number of initiatives, many of which were directed at increasing the membership. During that period, many new members were introduced to the Society, particularly in the category of Student Members. By

August 1997 the membership had risen to 404, and by June 2000 to 408.

Regarding the encouragement of Student Members, one initiative of Council was to hold an annual Postgraduate Symposium. The inaugural Postgraduate Symposium was held on 27th March 1999. As an incentive for postgraduates to present their work at the Symposium, initially a 50% discount on membership of the Society was offered, but it was not compulsory that students became members in order to present papers. Later presenters were given free student membership of the Society for one year. Symposia have been held annually since 1999, and now extended abstracts are published in the JRSWA.

Today, the Society has around 250 members, including Institutional/Corporate Members who subscribe to obtain the Journal. The decline in membership from that in 2000 has been of great concern to the Council of the Society. Council continues to develop strategies to combat the situation and project the Society to the wider community.

ROLE OF THE RSWA

Initially, the Society was established as the peak, multidisciplinary, scientific body in Western Australia, a role that it continues to play to the present day. Promoting the advancement of all branches of science is its principal role, and this is enshrined in the Society's Constitution. Unlike the Royal Society, which is used by the British Government as its principal source of independent scientific advice, the RSWA has never been regularly consulted by the State Government. Occasionally, individual members (in their own professional capacities and via their own institutions) have been involved in governmental advisory committees, but not as representatives of the RSWA. The Society has, however, made many submissions to Government and Government Agencies concerning scientific issues of the day (Griffin & Semenuik 1998), and currently has a permanent representative on the Council of the National Trust (WA), dealing with issues of preservation and conservation.

During its early years, the Society focused solely on scholarly research. Society meetings were devoted to sharing knowledge, and its 'flagship', the Journal, was the outlet for communicating such research. Additionally, the activities of the Society were frequently publicised by the local media. However, over the century of its existence the Society has gradually acquired, or assumed, other scientifically related roles, most notably, a greater interactive role with the community at large, and science education. For many years, general meetings of the Society have been open to non-members, and through this the Society has gained closer contact with the general public. Activities of the Society include lectures, small symposia and field excursions: during its early years, it also held exhibitions and screened films.

The Society, as a body, has often commented on government policies concerning science, or issues of the day requiring scientific input. Griffin & Semenuik (1998) listed 13 submissions in the thirty years between 1963 and 1993 concerning issues of land management and administrative procedures where they impinged on flora

and fauna, and on the general quality of science in Western Australia.

Since 1998, the RSWA has made a number of important submissions including: (i) 1998 a submission regarding the Regional Forest Agreement; (ii) 2000 submissions on the terms of reference for the Review of Sustainability Yield in SW Native Forests, and the Chief Scientist's Report – 'The Chance to Change'; (iii) 2001 a submission to the Inquiry into the Regional Development of Bioprospecting Industries; and (iv) 2002 a submission regarding taxonomic research on Australia's biodiversity as a nomination for the National Research Priorities.

For a number of reasons, in recent years, this advisory role of the Society has gradually diminished. One reason is that many member scientists are employed in the Public Sector and are reluctant to comment on Government policies, even though their views would be presented by the Council of the Society and not as individuals.

In April 1997, the then Deputy Premier, The Hon Hendy Cowan MLA, launched the State Government's first Science and Technology Policy, and a portfolio for Science and Technology was added to the responsibilities of the Deputy Premier. In the previous year, Cowan had spoken to a full meeting of the RSWA, and had also talked to the Council about the Government's initiatives for science and technology.

Following a change of government, The Premier, Hon Geoffrey Gallop MLA, then Minister for Science, addressed the Society about the WA Premier's newly formed Science Council and the Government's vision of science for WA. Later a revised portfolio of Minister for Environment and Science passed to The Hon Judy Edwards MB BS MLA. Taking up a suggestion made by Griffin & Semeniuk (1998), in August 2005, the author as President and several Councillors initiated monthly meetings with the Minister for Environment and Science and her advisors.

Meetings focused on science in the State. At the first meeting the Minister was informed of the range of activities undertaken by the RSWA, and its principal role in promoting science and scientists. The Minister outlined the development of science policy for that term of government. In response, RSWA delegates outlined ways in which the Society, as an apolitical, multidisciplinary scientific group could help the Government. The thrust of science policy then (including the Science Council and Chief Scientist) was aimed at large applied science projects, with big budgets and clear economic benefits. The Society was keen to emphasise the other end of the scientific spectrum and suggested that the investment of relatively small amounts of money, well directed into basic research, would ultimately be beneficial to science in the State.

The Society stressed the importance of recruitment and retention of young scientists graduating from the State's universities into State-funded research institutions, and a number of relatively inexpensive measures were identified that the Government might consider. These included stipends for graduate and postgraduate students to undertake work in State-funded institutions during the summer period, and the establishment of competitive, short-term Junior Doctoral

Fellowships. A much larger issue concerned the non-medical scientific public service, which was recognised by the Society as long overdue for review.

Following Minister Edwards' resignation in January 2006, meetings with her successor, The Hon Francis Logan MLA, were rearranged on a bi-monthly basis for 2006. The new Minister for Science did not have responsibility for the Environment, which was made into a separate ministry. Eventually meetings with the Minister ceased.

RSWA LIBRARY HOLDINGS AND LIBRARY EXCHANGES

Since 1960, through a written agreement with the then Director of the Western Australian Museum, W D L Ride (President 1962–1963), the RSWA Library has been held in trust by the Library of the Western Australian Museum. Moreover, from that time, the Museum's Librarian became *de facto* Honorary Librarian of the RSWA. Originally, the RSWA Library was held in Perth, however in 2004 with the imminent closure of the Museum's Francis Street building, the library was moved to the ground floor of the Administration Building of the Museum's Research and Collections facility at 49 Kew Street, Welshpool. During her tenure as Honorary Librarian (1987–2012), Margaret Triffit brought the RSWA library and Museum's own library into the electronic age.

The RSWA Library is an important collection of specialist books, journals and other scientific publications. The great majority of the titles have been obtained by exchange for the IRSWA, and some are unique holdings in the State. The Library also contains more than a hundred monographs published prior to 1900, many acquired by donation. The titles include several rare publications on early voyages to Australia, and the botany of Australia. Overall there are some 350 books and 980 journal titles of which more than 300 are current. In 2000, a combined WA Museum and RSWA Library Catalog was released on CD-Rom including fully searchable records for over 18 000 monographs, 2700 journal titles and 2200 indexed reprints/articles on molluscs, many published more than 50 years ago. Today catalogues of the RSWA publication collection (along with the Museum's own holdings) are available on line through the WA Museum's website (http:// library-srv.museum.wa.gov.au/menu.htm). Borrowing from the Library is restricted to Museum staff. However, the RSWA Library is available to the public for reference and research, and articles may be photocopied. The Library can be accessed by prior appointment with the Librarian.

MANAGEMENT

The management of the RSWA is vested in an elected Council comprising a President, two Vice-Presidents, the immediate Past President, Treasurer, Librarian, joint Honorary Secretaries, Honorary Editor(s) and eight Council members. Originally, the two secretaries were appointed to represent the physical and natural sciences, respectively. Later the secretaries took on specific roles;

one acting as secretary to Council, and the other as the secretary responsible for the Proceedings and other duties relating to general meetings. Later, an additional secretary was co-opted from Council to deal specifically with membership matters.

From about the 1940s with few exceptions, the line of succession for President of the RSWA was decided by the election of Junior and Senior Vice-Presidents. The President may serve up to a maximum of two years and upon the end of the President's term of office the Senior Vice-President would assume the role of President (provided there was no challenge) at the Annual General Meeting, the Junior Vice-President would be elevated to Senior Vice-President, and a new Junior Vice-President elected from Council. Generally, though not always, this line of succession (accepted by the membership of the Society) served the Society well, ensuring that experienced Councillors and those well versed in the management of the Society became Presidents and other senior officers.

In September 1998, Council decided to elect an Honorary Publicity Officer from the Council membership. The role of the Publicity Officer was to keep the Society, and science in all its aspects, in the public view, and to raise the consciousness of the public, decision makers and politicians, in regard to the Society's activities and intellectual resources.

In 2011, as the result of internal divisions, Council resolved to call an election for all positions on Council, and a ballot of the membership was held. The outcome was that previous informal positions held by Councillors for specific tasks, such as Publicity Officer, Webmaster, and Archivist, ceased to exist.

During the mid-1960s, notably through the work of Duncan Merrilees (Vice-President 1964-1966 and President 1966–1967), changes were made to the Society's Constitution to bring it in line with modern practice. In June 2011, Council resolved to propose five significant changes to the Constitution, and these were put to a ballot of members as part of the election process. The changes were subsequently accepted by the membership. These changes concerned: the standing of Student Members in the Society; subscriptions; the timing of General Meetings; the means by which the Constitution or rules and regulations of the Society may be changed; and the inclusion of definitions under rule 1 of the Constitution. The latter brought the Constitution in line with guidelines (Department of Commerce 2010) of the State's Department of Commerce concerning Incorporated Associations.

On 29 July, 2011, a forum was held to discuss some concerns held by a number of members regarding the AGM and elections to Council. A summary of the forum was later provided by Associate Professor John Bailey and published in the Proceedings of the Society (Bailey 2011). The forum agreed to continue with the election ballot (then underway), and it was proposed to establish a tripartite Review Panel to inquire into matters raised before and at the forum concerning the Society's governance. No agreement could be achieved as to the composition of the Review Panel and, subsequently, the newly elected Council deemed it was unnecessary and the review did not proceed.

MEETINGS VENUES, AND THE QUEST FOR A PERMANENT HOME FOR THE RSWA

Prior to the establishment of the RSWA, forerunner societies held meetings in at a variety of venues. In 1905, the West Australian Natural History Society established its headquarters at the Western Australian Museum, but in 1909 it had to move from that venue and some meetings had to be cancelled for a lack of a meeting room. Later, rooms of the Theosophical Society were made available on the third floor the West Australian Chambers in St George's Terrace at a weekly rent of 10 shillings. It was at this venue that the RSWA was established. The Society's library and herbarium were also housed at the venue and the rent was later raised to 30 shillings.

Early in 1916, the Society had to move from rooms of The Theosophical Society and fortunately accommodation was again provided by the Museum. The Society remained at the Museum until July 1940 when it relocated to the seventh floor of the University of Western Australia (UWA)-owned Gledden Building on

the corner of Hay Street and William Street (Figure 7). The Institute of Engineers leased the top floor of the building and accepted the RSWA as a sub-tenant, initially for a rent of £30 per annum (Jenkins 1965).

The Society occupied the Gledden Building rooms for 17 years by which time the rent had risen to £100 per annum. In 1957, UWA terminated the Institute of Engineers' lease and the Society had to find new accommodation. Serendipitously, the Museum was undergoing an expansion, and the Society was once again able to secure rooms there. This provided the Society with the accommodation and facilities it had long sought. During the period 1957-1971 General Meetings of the Society were held regularly in the Woodward Gallery at the Museum. Other venues at various Universities were used when larger audiences were anticipated, or when joint meetings were held with other societies and associations, such as the WA branch of ANZAAS. From March 1971 until July 1973, the RSWA held regular meetings at Science House, 10 Hooper Street, West Perth, the new home of the Institute of Engineers, where parking was evidently much easier than near the Museum (Jenkins 1965).



Figure 7 The Gledden Building, 731 Hay Street, Perth. Home to the RSWA 1940–1957. (Courtesy of Wikipedia).

In July 1973, the AGM of the Society was held at Mineral House, Adelaide Terrace, the home of the Geological Survey of Western Australia. Until June 1978, Mineral House became the regular venue for General Meetings, with occasional meetings at other venues.

In June 1978, the venue for meetings moved to the Kings Park Board Room. Initially alternating with the Mineral House venue, eventually the Board Room in the Kings Park Administration building became the principal venue and remains so to the present day.

From the outset of the Mueller Botanic Society, representations were made to Government to obtain a grant of land on which a permanent home for that Society could be built. As early as 1897 funds were sought from the State Government to employ a secretary, a professional botanist and a librarian.

This request was not granted. Again in 1916, representatives from the RSWA and other institutions, including the Institute of Engineers, presented a case to Government for a land grant to no avail. In 1927, in light of the Government's decision to undertake a scheme of building to celebrate the State Centenary, the RSWA convened a meeting of interested societies and associations to draw up a petition to Government for the acquisition of land, and the provision of a suitable building to be shared by various scientific workers in the State. The associations included the Chemical Society, the Engineering Standards Society, the West Australian Field Naturalists Club, the Historical Society, the Economic Society of Australia & New Zealand, the League of Nations Union, the West Australian Society of Arts, the British Astronomical Association (WA Branch), and the Town Planning Association. In the 1929 Annual Report of the RSWA the Secretary records " at present there seems little prospect of securing adequate accommodation for no Government funds are available."

In this regard, the Government overlooked an opportunity to create in Perth an approximate equivalent to Burlington House in London, which is home to many learned societies of both arts and sciences. In 1936 while the RSWA entered into negotiations with the Institute of Engineers regarding rooms in the proposed University Gledden Building, negotiations by the Society (through its Honorary Solicitor) to obtain land in Irwin Street failed, but the Society was directed to land on the corner of Beaufort and James Streets, and to blocks opposite Perth Boys' School. All negotiations for these sites failed. In 1957, the Institute of Engineers approached the RSWA regarding the possibility of a joint purchase of a house (later 'Science House') in West Perth. At that time an arrangement with the Museum for accommodation was in train, and the Society declined the offer. Nevertheless, the Society would later use 'Science House' for meetings.

The RSWA still does not have a permanent home, although it currently has an office at Curtin University, and a part-time paid secretary funded by the Society.

ROYAL SOCIETIES OF AUSTRALIA

At various times during its history the RSWA has sought to forge stronger ties with other State Royal Societies. In 1918, the Society was represented by Sir Edgeworth David and Mr J H Maiden at a conference of Australian Royal Societies convened by the Royal Society of New South Wales at the request of the Royal Society (in London). This conference led to the later formation of the Australian National Research Council and eventually the Australian Academy of Science (Jenkins 1965).

At another conference in 1930 under the auspices of the Royal Society of Victoria, Professor Wilsmore represented the RSWA to consider the formation of a 'Royal Society of Australia', or a federation of State Royal Societies. The proposal was further considered at the meeting of the Australian and New Zealand Association for the Advancement of Science (ANZAAS). The proposal for a 'Royal Society of Australia' was not favoured because of the possibility it might lead to the State Royal Societies losing their individual identities. A Royal Society was formed in Canberra in 1930 and assumed the name 'Royal Society of Australia'. The State Societies were strongly opposed to this title, and in 1955 it was changed to the Royal Society of Canberra (defunct since 1973).

In 1945, the RSWA put forward the proposal to other State Royal Societies that reciprocal rights be offered to members travelling interstate. This was unanimously accepted giving all members of the six Societies the privilege (without voting rights) of attending meetings in other States.

The matter of a 'Royal Society of Australia', or other form of alliance, lay dormant for another seven decades until in December 2004, under the auspices of the Royal Society of New South Wales and with the President of that Society, Karina Kelly in the Chair, a Convention of Presidents and other delegates of the six State Royal Societies was held in Sydney to discuss how they could co-operate more closely. The RSWA was represented by the author. The formation of a 'Royal Society of Australia' was rejected on similar grounds to the proposal in 1930: however, there was general agreement that a closer alliance would be beneficial to all Societies. An umbrella organisation was proposed with the name 'The Royal Societies of Australia' to emphasise an alliance without further commitment, and without impinging on the individual identities of the six Societies.

Following the Convention, a reception was held at Government House in Sydney hosted by the Governor General, His Excellency Major General Michael Jeffery AD MC, and in the presence of Her Excellency, Professor Marie Bashir AC CVO, Governor of New South Wales and Vice-Patron of the Royal Society of NSW.

In the following year, a second Convention was held in Melbourne under the auspices of the Royal Society of Victoria. Again the author represented the RSWA as its President. At this Convention neither the RSSA nor the RSQ was represented. Discussions followed along much the same lines as the first Convention, and it was agreed that a more formal 'Royal Societies of Australia' alliance could be beneficial with the main purpose of raising the awareness of the work of the Royal Societies in the wider Australian community, and to assist the activities of the State Royal Societies in Australia through organised collaboration.

The Royal Societies of Australia (RSA) was incorporated as a company limited by guarantee on 3

August 2007 and the first President was W J W McAuley. His Excellency The Governor General of the Commonwealth of Australia acts as Patron. The first formal convention of the RSA was held in Canberra on 2 February, 2008 with delegates representing the RSNSW, RSSA, RSV, RSQ and RSWA. The President of the Royal Society of New Zealand attended as an observer.

Today, the RSA representatives comprise the President, John Hardie (RSNSW), Honorary Secretary, Philip O'Brien (RSWA), Honorary Treasurer, Lynne Milne (RSWA) and Councillors, Clive Wilmot (RSNSW) and the author (RSWA).

In November 2008, a Convention of the RSA attended by representatives of the RSV, RSNSW, and RSWA was held at the Weld Club in Perth. The RSWA was represented by the then President, Philip O'Brien, and the author as Immediate Past President. A draft constitution for the alliance was discussed and circulated for comment. Subsequently, however, internal changes in the RSV, RST and RSSA saw them withdraw from any proposed alliance, leaving only the RSNSW and RSWA as interested partners. The membership of the RSQ had dropped to a very low number and the Society was in danger of becoming defunct. In an attempt to rekindle the interest of the RST in the RSA alliance, a Convention was held in Hobart in 2009.

In order to assist the RSQ, an AGM of the RSA was held in Brisbane in November, 2010. The RSWA was represented by the then President, Lynne Milne, and the author by teleconference from Perth. The RSNSW was represented by their President John Hardie (and President of the Royal Societies of Australia) and Clive Wilmot.

TO THE FUTURE

The RSWA has evolved considerably during the 100 years of its establishment and much has been achieved. However, like all societies, the RSWA continues to face the challenges of a fluctuating, but not significantly enlarging membership, and in maintaining its relevance in modern-day society. In essence, the primary role of the Society to promote science has not changed: what has changed significantly is the method of delivery. The Journal, Proceedings and Library Catalogue are now all available in electronic form. It is possible to join the Society, and to gain information about its activities on line through the Society's website (http:// www.rswa.org.au/). Membership is open to all those interested in science, and electronic access to back issues of the Journal is free.

In this electronic age, there is no doubt that the future lies in faster communications and more easily accessible electronic resources. The Society should continue to engage with politicians, Government, and the wider community regarding the importance of science to society. To this end the Society should develop a "Register of Scientists" for the Society's website (one was first published by the Society in 1995), to be a source of specialised knowledge and commentary.

If the Society is to thrive through this century, then it will be through the endeavours of successive Councils to develop strategies of engagement with its membership and beyond. The Society should create forums on controversial scientific matters of the day, and to take a more active role as a scientific watchdog in these challenging times.

ACKNOWLEDGEMENTS

The author is indebted to Philip Withers and Tony Cockbain for information provided, and to John Glover and Phillip Playford for reviewing the paper and providing many helpful suggestions for its improvement. Jenny Bevan is thanked for criticising an earlier version of the manuscript.

REFERENCES

- Bailey J 2011. Royal Society of Western Australia Governance Review. *Proceedings of the Royal Society of Western Australia* August 2011, 2.
- Bradshaw S D (Editor) 1983. Research on Rottnest Island. *Journal of the Royal Society of Western Australia* 66(1, 2), 1–61.
- Brocx M & Meney K (Editors) 2011. Symposium on Kimberley Marine and Coastal Science. *Journal of the Royal Society of* Western Australia 94(2), 55–418.
- Browne M A 1914. The approximate summation of series in which each term is a function of the corresponding term of an arithmetical progression. *Journal of the Royal Society of Western Australia* 1, 1–7.
- DEPARTMENT OF COMMERCE 2010. INC. A guide for incorporated associations in Western Australia. Department of Commerce, Perth.
- GRIFFIN S & SEMENIUK V 1998. The role of the Royal Society of Western Australia in the advancement of science. *Journal of the Royal Society of Western Australia* 81, 77–84.
- Jenkins C F H 1965. A history of the Royal Society of Western Australia, and its role in the community. Presidential Address. Journal of the Royal Society of Western Australia 48, 33–44.
- Kimberly W B 1897. History of Western Australia, a narrative of her past together with biographies of her leading men. Niven & Co, Melbourne.
- LEFTWICH P 1950. In Memoriam, Dr Stephen King Montgomery. South African Medical Journal 24, 182–183.
- McComb A J (Editor) 1973. The south-west of Western Australia. Journal of the Royal Society of Western Australia 56(1,2), 1–64.
- MENEY K & BROCX M (Editors) 2009. Leeuwin Current Symposium 2007. Journal of the Royal Society of Western Australia 92(2), 31–241.
- MENEY K & BROCX M (Editors) 2009. Evolutionary Biology Symposium. Journal of the Royal Society of Western Australia 92(4), 365–487.
- Montgomery S K 1919. Some Hymenosomidae from the Swan River. Journal and Proceedings of the Royal Society of Western Australia 6, 93–96.
- Summers L 1982. A guide to the minutes and correspondence series of the Royal Society of Western Australia, Inc. Diploma of Information Management Thesis, Archives Administration, University of New South Wales, Sydney (copy available in the Royal Society of Western Australia Library, Western Australian Museum).
- Traylen W M 1924. Unpublished manuscript. Battye Library, Perth.
- WITHERS P C 1998. A brief history of the Journals, Crests, Medal and Seal of the Royal Society of Western Australia and previous Societies, 1897-1997. Journal of the Royal Society of Western Australia 81, 1–4.

Received 29 May 2013; accepted 9 August 2013

Maritime archaeology in Western Australia

JN GREEN

Department of Maritime Archaeology, Western Australian Museum, Cliff Street, Fremantle WA 6160, Australia.

⊠ jeremy.green@museum.wa.gov.au

Western Australia enacted the world's first underwater cultural heritage legislation in 1963, that protected any site dating before 1900. This legislation was a result of concern by some finders of several important Dutch East India Company shipwrecks that looting was taking place. The finders appealed to the State Government to protect these sites and as a result what became the Maritime Archaeology Act was passed. The Western Australian Museum was given responsibility for these sites. In the beginning the management was complicated because at that time there were few properly trained maritime archaeologists in the world. Eventually in the early 1970s the Museum established a properly equipped conservation laboratory to deal with artefacts from shipwrecks and a department of maritime archaeology. This paper discusses the development of the work of the Museum on shipwrecks on the Western Australian coast.

KEYWORDS: conservation, excavation, legislation, maritime archaeology, survey.

INTRODUCTION

In 1963, following the discovery of two VOC (Vereenigde Oost-Indische Compagnie, Dutch East India Company) shipwrecks, the government of Western Australia amended the Museum Act to protect all shipwrecks that occurred before 1900. This was the first legislation, anywhere in the world, that specifically protected underwater cultural heritage. This legislation, however, was not amended at the whim of government; it was the result of a number of private individuals lobbying the government to protect sites that were being looted. In early 1963, newspapers in Western Australia abounded with reports of looting and conflict on the wreck sites, particularly the Vergulde Draeck, which lay just over 100 km north of Perth. Following these events, a group of the finders approached the State Government suggesting that they were prepared to relinquish their rights as finders, provided the Government enacted legislation to protect the sites. The Government agreed, and amended legislation to protect all shipwrecks. This was the first underwater cultural heritage legislation in the world.

LEGISLATION

The history of the Western Australian Museum's involvement in maritime archaeology started in 1963. It was then that the Western Australian Government passed an amendment to the *Museum Act 1959 (WA)* giving to the Museum responsibility for shipwrecks that occurred prior to 1900, and in the territorial waters of the State. This legislation came about, firstly, as a result of an initiative of the finders of the *Vergulde Draeck* and the *Batavia* (Drake-Brockman 1963; Edwards 1966), who passed their rights, as finders, to the Government; and, secondly, because these sites were being looted and vandalised, causing a public outcry. The Act gave the Museum authority to control and administer the wreck sites on the Western Australian coast. At that time, the concerns were purely for the Dutch shipwrecks and

interest in the post-settlement wreck sites was to come later.

It is not surprising that the legislative pathway was complex as it was without precedent. Remember that this was the first legislation anywhere in the world to protect underwater cultural heritage, reaffirming the position taken in the early Western Australian initiative to protect sites and heritage.

In 1972, after negotiations between the governments of the Netherlands, the Commonwealth and the State, the Australia Netherlands Committee on Old Dutch Shipwrecks (ANCODS) Agreement was signed. Under this Agreement the Netherlands Government, as heir to the United Dutch East India Company (VOC), agreed to transfer to the Australian Government any rights of claim the Netherlands might have to the VOC shipwrecks. The Agreement required that a committee be formed that would oversee the operations of the Museum and that representative collections would be selected for the Netherlands and Commonwealth Governments, with the understanding that the bulk of the collection would remain in the Western Australian Museum (Bolton 1977). In 1973, there was a further legislative change and the historic wreck provisions were removed from the Museum Act and incorporated into a new Maritime Archaeology Act 1973 (Western Australian Consolidated Acts 2010). Meanwhile, concern was being expressed in legal circles about the validity of the State Act, which came to a head finally, in 1976, following a challenge in the case of Robinson v Western Australian Museum. when the High Court of Australia ruled that the State Act was invalid (Kennedy 1998). As a result of this decision the Commonwealth's Historic Shipwrecks Act 1976, which had been prepared before the High Court challenge was heard, was proclaimed to apply in the waters of Western Australia. In fact, there were a few days between the High Court decision and the proclamation of the new act when the wrecks in Western Australian waters were not protected under any form of legislation. Ironically, this hiatus occurred in the middle of the First Southern Hemisphere Conference on Maritime Archaeology, which was being held in Perth. Following this landmark

decision, the *Historic Shipwrecks Act* proclaimed in the Commonwealth Waters off the Western Australian coast had jurisdiction from the low-water mark to the edge of the Exclusive Economic Zone. Western Australia's *Maritime Archaeology Act* applied in State waters, which included rivers and enclosed bays and sites above the low-water mark. The complexity of the dual jurisdiction, as it applies in Western Australian waters, lies in the fact that the concept of State waters still exists, extending out three nautical miles from the coast.

While the State legislation does not apply to things on or below the seabed, it does apply to things in the water column such as fish. So most State legislation, apart from shipwrecks, now applies out to the three-mile limit and is a curious anachronism. Other Australian States followed a similar process of proclamation, but as they did not have specific legislation covering underwater cultural heritage they enacted 'mirror' legislation to apply to their State waters (legislation that was essentially the same as the Commonwealth Act). In Western Australia, the State Act is vastly different from the Commonwealth legislation. The protection provided by the Historic Shipwrecks Act 1976 for underwater cultural heritage differed markedly from that offered by the Maritime Archaeology Act. Whereas the State Act protected archaeological sites, the Federal legislation was directed towards protecting shipwrecks and associated relics. Initially, the Historic Shipwrecks Act gave no specified date to define 'historic' in relation to a shipwreck. To gain protection for a wreck, it was necessary to provide a justification to the Minister as to why the site should be protected. This proved to be unwieldy in implementation, particularly as it caused delays between the discovery and the gazettal, during which period the site was not protected. A number of amendments have been made to the Federal Act since its enactment, including one that introduced a rolling date, so that sites that are older than 75 years are automatically protected. The differences between the State and Federal legislation still create anomalies though, as in the case where a wreck lies partially in Commonwealth waters and partially in State waters. The Commonwealth section (i.e. the part below the low-water mark) is protected if it is more than 75 years old, but the other part, above the low-water mark, will not be protected under the State Act unless its date is earlier than 1900.

Another legislative issue that arose was the question of rewards, The Commonwealth Act leaves the discretion of reward to the Minister with the general attitude that rewards for reporting a site are inappropriate, citing the example we do not usually reward people for obeying the law. The Maritime Archaeology Act 1973 included a provision to reward the finders of shipwrecks, and the reward process was clearly laid out. However, this provision was not made retrospective; thus, the finders of wrecks already discovered, including the Batavia, Vergulde Draeck, Zeewijk (Edwards 1970), Zuytdorp (Playford 1996) and the Cottesloe Wreck (Elizabeth), were not eligible for such a reward. This proved to be a highly contentious and on-going issue, both for the finders and in the perception of the general public, and the matter was only finally resolved in 1994 by the findings and recommendations of the Western Australian Government Select Committee on Ancient Shipwrecks (Pendal 1994). The Committee recommended that any person who reported their discovery of a wreck site should be rewarded; and that the early finders of wreck sites, who had been deprived of rewards, should be properly acknowledged and rewarded. These findings were incorporated in the Third Schedule (Section 24) of the Maritime Archaeology Act 1973, in 1997 (Western Australian Consolidated Acts 2010).

While the legislation is undergoing review at both State and Federal levels, another important development has been the UNESCO Convention on Underwater Cultural Heritage. This international Convention was adopted in November 2001, with WA Maritime Museum Director, Graeme Henderson, in the role of chair of the ICOMOS International Committee on the Underwater Cultural Heritage (ICUCH) which instigated the Convention. The Convention requires that countries enact enabling legislation, which, in the case of Australia, will require all States and the Commonwealth to rewrite their respective Acts. It is, however, a landmark decision in that it clearly indicates that underwater cultural heritage should be protected, reaffirming the position taken in the early Western Australian initiative to protect sites. It is still unfortunate that Australia has been unable to ratify the UNESCO Convention, while many other countries have. The amendments to bring the State up to date have been awaiting Government initiative to start the process for over 20 years. These amendments will also be required in the process of ratifying the Convention

1960S AND THE EARLY BEGINNINGS

Following the enactment of the State legislation, the Museum began to establish an administrative structure to look after the shipwrecks under its jurisdiction (Figure 1). Since there was no similar situation elsewhere in the



Figure 1 Map of selected wreck sites.



Figure 2 Batavia wreck site (WA Museum © photo BTA0708).

world that could be used as a model, the Museum initially adopted a holding operation on the sites, rather than starting excavation or salvage. Additionally, there were no trained maritime archaeologists in Australia and only a few European countries had experience in this area; hence there was no precedent for establishing a maritime archaeological programme. In what was acknowledged to be an unsatisfactory situation, the general public complained that nothing was happening, whilst amateur divers felt that they could, and therefore should, do the work. The Museum came under growing criticism over the lack of action (Crawford 1977).

In 1967, Colin Jack-Hinton was appointed as the head of a newly created Division of Human Studies at the Museum; under his direction, resources were acquired and staff recruited. A watch-keeping operation was established on the two most important threatened sites, the *Batavia* (Figure 2) and the *Vergulde Draeck* (Figures 3–5), providing accommodation facilities, boats and diving equipment. The Museum also sought advice on how a maritime archaeological programme should be run. In the late 1960s, a Historic Wrecks Advisory Committee was established to help advise on the direction of the programme and counter some of the criticism the Museum was attracting. This Committee, in its various manifestations, exists today as the Maritime Archaeology Advisory Committee and still meets regularly.

In the late 1960s, G. van der Heide from the Ijselmeerpolder Museum in the Netherlands came to Perth at the invitation of the Museum to advise on how best to manage the programme. Staff were sent to the Netherlands to work with the excavation of the shipwrecks in the polders, but at that time no underwater archaeology was being done in the Netherlands, or for that matter anywhere else in the world except for a few



Figure 3 Complex cave system on *Vergulde Draeck* wreck site cannon leaning upright in background (WA Museum © photo GDA211).



Figure 4 Astrolabe from Vergulde Draeck wreck site (WA Museum © photo GDA328).



Figure 5 Beardman jugs and reals of eight from *Vergulde Draeck* wreck site (WA Museum © photo GDA5_065).

cases. This was the beginning of a long and fruitful cooperation between the Museum and scholars in the Netherlands.

In 1969, Ian Crawford took over as Head of Division of Human Studies. By that time, a limited excavation had started on the *Vergulde Draeck* and in 1970 a joint Museum and University of Western Australia expedition carried out a survey and limited excavation of the *Batavia* wreck site. In 1970, David Ride, the Director of the Museum, made a submission to the Western Australian Government that it provide appropriate support for the maritime archaeological programme. The support was forthcoming and resulted in the appointment of Colin Pearson as Head of the Conservation Laboratory, and the appointment of Jeremy Green in 1971, as Head of the Department of Maritime Archaeology.

1970s: THE DEPARTMENT IS ESTABLISHED

With proper conservation facilities and the resources to carry out major excavation projects, the scene was set for a new initiative in maritime archaeology. A custom-built 12 m workboat, the *Henrietta*, was built and new curatorial staff were recruited to complement the existing technical staff. By 1972, the Department numbered about 15 people. They had a new office in Fremantle, alongside the Conservation Laboratory, and there were field stations on Beacon Island, in the Houtman Abrolhos, and at Ledge Point, north of Perth. The first project was a



Figure 6 Trial wreck sites showing anchors (WA Museum © photo TRA112).

survey of the Trial wreck site (Figure 6) (Green 1977a). (It should be noted that in contemporary documents the name of this ship was spelt four different ways, often two different ways in the same document. I have chosen the first and most common spelling of the name, the others being Triall, Tryal and Tryall.) After the survey of the Trial an excavation of the Vergulde Draeck site was undertaken (Green 1977b). By the end of the Vergulde Draeck excavation, the departmental team was experienced enough in shallow-water surf-zone excavation to start work on the Batavia. The Vergulde Draeck had been chosen first for excavation, because of its proximity to Perth and because the site was under greater threat than the Batavia. The Batavia, however, was a much bigger project; not only was the site a lot larger and more complex, but the logistics of working in the remote Houtman Abrolhos was extremely demanding (Drake-Brockman 1963). Work started on the Batavia site in December 1972, the first of four excavation seasons (Green 1989). In total, approximately 450 days of fieldwork were logged on the Batavia project. During the course of the excavation, it became clear that a large intact section of the ship had survived and it was decided to raise this section for conservation. This inevitably led to the question of where the raised section (measuring some 30 m x 10 m x 6 m) could be housed. Fortunately, Fremantle in the late 1970s was fruitful ground for such a quest. There was a large, derelict heritage building—the Commissariat Building—that was found to have a room of suitable size to house the reconstruction. Indeed, the

building was spacious enough to house a large number of exhibition galleries as well as the respective Departments of Maritime Archaeology and Materials Conservation.

The refurbishment of the Commissariat Building was carried out by the Public Works Department and won numerous heritage awards for the quality of the restoration. The building was officially opened in 1979, housing the restored *Batavia* hull and portico façade and exhibitions of material from the wreck sites investigated by the Department.

At the end of the Batavia project, work started on a post-settlement maritime archaeological programme under the direction of Graeme Henderson, who was then a curator in the Department. Initially, when the Museum started its programme in maritime archaeology, the current thinking was that the Dutch wrecks were the most important sites. The later, early 19th century and post-settlement, sites were thought to be relatively insignificant at the time. The Department became increasingly concerned, however, at the public perception that the Museum was not interested in these sites, which was leading to widespread looting of many of them. It was recognised that these sites would prove immensely important to the early European history of Western Australia and of Australia, and a programme of work was developed for them. This started with excavations on the Eglinton, followed by the James Matthews, Rapid and Lively (Figures 7, 8).



Figure 7 Rapid wreck site showing coins (WA Museum © photo PCA39).



Figure 8 Excavating *James Matthews* site, roofing slats to left of scene (WA Museum © photo JMA54).

In 1974, Scott Sledge became responsible for the wreck inspection programme that monitored reports of wrecks and inspected the sites. In 1978 he led the very successful Wreck Inspection North Coast (WINC) expedition, which examined sites in the far north of the State. The wreck inspection programme was later taken over by Michael McCarthy.

INTO THE 1980s: DEVELOPMENT AND DIVERSIFICATION

The Department's Dutch wrecks programme did not finish with the excavation, conservation and reconstruction of the *Batavia*. It continued with work on the *Zeewijk* site (Figure 9), where several seasons of excavation and survey were carried out under the direction of Catherina Ingleman-Sundberg. Later, the Dutch wreck programme turned to the *Zuytdorp*, an incredibly difficult site to work (Figure 10).

On another front, McCarthy initiated a programme looking at iron and steam shipwrecks. This led to the First Australian Seminar on the *Management of Iron Vessels and Steam Shipwrecks*, which was held in 1988 (McCarthy 1988). McCarthy's important excavation of the steamship *Xantho* (Figures 11, 12), with the subsequent recovery of the vessel's engine, started yet another interesting and exciting initiative for the Department. The dismantling of the concreted and corroded engine, and its subsequent conservation process, has provided new insights into the study of iron shipwrecks and their conservation.

Land archaeological work associated with maritime activities is another branch of research within the Department. Myra Stanbury has undertaken research of the guano industry in the Abrolhos, as well as studying the whaling industry, particularly at the Norwegian Bay Whaling Station at Point Cloates and pearling in the Monte Bello Islands. Myra's main responsibility has been the management of the Department's artefact collection and research, and publication of sites that the Department has previously worked on. The Department has been involved in numerous land archaeological projects, particularly where they interface with the maritime milieu.

In 1981 Michael McCarthy initiated Australia's first wreck access program, which has since developed into an outreach programme. The objective of such programs is to provide information for the public as well as opportunities for them to look at and enjoy shipwrecks. Through public involvement and introducing the concepts of an 'Underwater Museum' where the wreck sites are the 'show cases' and the ethos is 'please enjoy—look but don't touch', the Department encourages the concept of protecting sites for future generations.

Other avenues for public involvement in maritime archaeology include the Maritime Archaeological Association of Western Australia (MAAWA), an amateur organisation founded in 1974 (Robinson 1977). This Association assists the Department in projects and played a particularly important role in the excavation of the *Batavia* and the other early departmental projects. It also conducts its own programmes and has a long and



Figure 9 Surveying Zeewijk site with underwater theodolite (WA Museum © photo ZWA142).



Figure 10 View of Zuytdorp cliffs near wreck site (WA Museum © photo ZUYB08A).



Figure 11 Xantho engine after conservation (WA Museum © photo BTA0708).

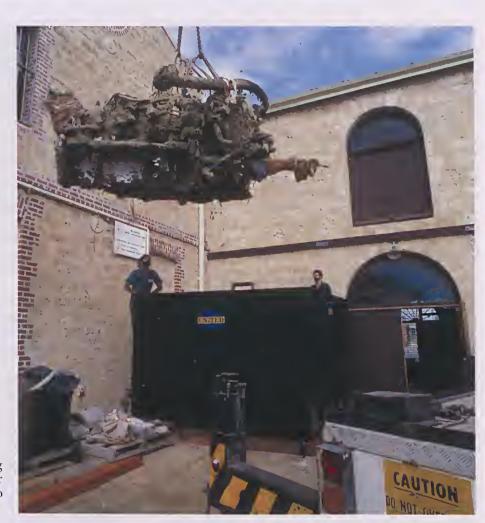


Figure 12 *Xantho* engine being loaded into conservation tank prior to treatment (WA Museum © photo BTA0708).

Table 1 List of significant Western Australian wreck sites

Name	Date	Place	Country
Trial	1622	Montebello Islands	English East India Co
Batavia	1628	Wallabi Group Abrolhos	VOC
Vergulde Draeck	1656	Ledge Point	VOC
Zuytdorp	1712	North of Kalbarri	VOC
Zeewijk	1727	Pelsaert Group, Abrolhos	VOC
Lively	1810	Rowley Shoals	British, ex French
Rapid	1811	Point Cloates	American
Correio da Azia	1816	Point Cloates	Portuguese
Belinda	1824	Middle Island, Recherche Archipelago	British
James	1830	Cockburn Sound	British
Cumberland	1830	Hamelin Bay	Indian
Thames	1830	Fremantle	British
Emily Taylor	1830	Fremantle	British
Grey's whaleboats	1839	Kalbarri	Australian/American
Lancier	1839	Stragglers	Mauritius
Elizabeth	1839	Cottesloe	British
Samuel Wright	1840	Bunbury	American
North America	1840	Bunbury	American
Persévérant	1840	Dirk Hartog Island	French
James Matthews	1841	Woodmans Point	British
Amelia	1842	Fremantle	British
HMAS Sydney II	1941	Continental Shelf	Australian
HSK Kormoran	1941	Continental Shelf	German

impressive publications record. Another relatively new initiative targeting the public, managed by Corioli Souter, are the Australasian Institute for Maritime Archaeology (AIMA) and Nautical Archaeology Society (NAS) training courses. As well as providing technical training in maritime archaeology, these courses raise awareness about shipwrecks and the issues relating to the preservation of underwater cultural heritage. The Department has played an important role in the Australasian Institute of Maritime Archaeology (AIMA) since it was first established at the Second Southern Hemisphere Conference on Maritime Archaeology in Adelaide in 1983. Taking a leading role in the formative years of the Institute, the Department still regularly produces and edits the annual AIMA Bulletin, now in its 30th year of publication.

THE 1990s

In 1994 the Federal Government announced in its cultural policy statement *Creative Nation* that the Western Australian Maritime Museum would be established as a National Centre of Excellence for Maritime Archaeology. Funding was provided for a three-year period to support a number of projects; the funding ended in 1998.

In January 1998, there were reports from the Shark Bay Shire that a French coin and lead seal had been discovered on the northern part of Dirk Hartog Island. The coin (an *écu* dated 1766) had been located with a metal detector in the area reputed to have been the site of St Aloüarn's annexation of Western Australia for France in 1772. A team, including staff of the Department of Maritime Archaeology, Centre for Archaeology, University of Western Australia, and volunteers, subsequently returned to the site and using a combination of remote sensing and traditional archaeological methods located and then excavated an intact bottle, complete with a lead closure or seal containing another French *écu* dated 1767.

In 1997 reports were received that a grave site on Beacon Island had been discovered and a sword recovered. This site was excavated in 1999 and found to be a mass gravesite containing the bodies of eight people including an infant of less than 3 months old. This finding highlights the potential for Beacon Island, which in contemporary documents was referred to as *Batavia*'s Graveyard. It is known that over 125 people were massacred following the loss of the ship (Ariese 2012).

INTO THE NEW MILLENNIUM

In 2002, the spectacular new Maritime Museum building was opened on Victoria Quay, complementing the Shipwrecks Museum in the Commissariat Building. The new Maritime Museum, evolving from the work of the Department is largely devoted to maritime history, and the Commissariat Building has become a shipwrecks museum devoted to maritime archaeology and conservation.

Further work was carried out at Cape Inscription in 2003 and concentrated on a site survey and further magnetometer work, and an assessment of four-wheel drive damage to the *Persévérant* site, a French whaler lost

on the northeast side of the island in 1841 (Green 2007). In 2004, the Correio da Azia, the earliest Portuguese shipwreck in Australia was discovered. It was an advice boat travelling from Lisbon to Macau in 1816 and was wrecked on Ningaloo Reef (Green 2011). Letters in the Lisbon archives include a report of the loss by the Captain and the report of a vessel, the Emillia, that was sent to chart Point Cloates, which at that time was a notorious navigational hazard for vessels sailing to China. Previous Museum expeditions failed to locate the site because of adverse weather and the difficulty of searching this reef area with a magnetometer in a regular search pattern. Fugro Airborne Surveys, a Western Australia survey company, agreed to conduct an aerial magnetometer search of the area where the vessel was thought to have been lost. The survey found two sites, one of which was the Correio da Azia, the other an as yet unidentified site.

The Deep Water Graveyard southwest of Rottnest Island, was investigated in 2001. UTS Geophysics, a local company, flew an aerial magnetometer survey over a section of the graveyard and produced some astounding results. Eight clear magnetic anomalies were located and an additional survey over the HMAS *Derwent* site showed that this vessel could be detected easily in 200 m of water. The graveyard is host to a wide spectrum of material, from utilitarian barges and dredges to the remains of graceful clipper ships that ended their days as coal hulks in Fremantle harbour before being scuttled. There are a total of 47 identified wrecks in the Rottnest Graveyard.

Much of the work and research of the Department has been published (see for example: Green *et al.* 2004; Henderson 1980, 1986; Henderson & Henderson 1988; McCarthy 2013; Worsley *et al.* 2008, 2012). Other information and reports can be found on the departmental publications website: < http://museum.wa.gov.au/maritime-archaeology-db/maritime-reports>.

The Future

The State government has generously supported maritime archaeology in Western Australia and as a result the WA Museum has a national and international reputation in the field. The Department of Maritime Archaeology provides advice and training in countries throughout the world. In particular maritime archaeological conservation plays an important role in this work, and as described above, the archaeology has to be supported by conservation. Again, the Department of Materials Conservation has a international reputation in research related to the conservation of maritime archaeological material. It is of course the whole process that has to be considered in assessing how underwater cultural heritage is managed in Western Australia. Assessment of the heritage comes first, a careful decision on the merits of excavation, the archaeological excavation, conservation of the material, collection management and ultimately the display of the material and the publication of the work. We are fortunate in having a dedicated museum in Fremantle that can display the results of this programme.

Sadly today the ability to mount large scale excavations like the *Batavia* excavation and others in the

1970s and 1980s are no longer possible. Financial restraints limit the amount of work that can be carried out. However, in 2013 the Museum, in conjunction with the University of Western Australia received an Australian Research Council Linkage Grant to reinvestigate the early work carried out by the Department of Maritime Archaeology. This project which includes and international research team will seek new insights into the sites and the collections using modern technology. This is an exciting project with implications for every maritime archaeologist who has excavated a site. In the mean time, every year new sites are reported to the Museum. Although we know that about 1500 ships were lost on the Western Australian coast only about 300 have so far been found. So we are hoping one day someone will report another Batavia!

REFERENCES

- ARIESE C 2012. Databases of the people aboard the VOC ships Batavia (1629) & Zeewijk (1727): an analysis of the potential for finding the Dutch castaways' human remains in Australia. Australian National Centre of Excellence for Maritime Archaeology Special Publication 16.
- BOLTON G F 1977. Legislation—What is ANCODS? (Australian Netherlands Committee on Old Dutch Shipwrecks). In: Green J N (ed.) Papers First Southern Hemisphere Conference on Maritime Archaeology, Pertli, Western Australia, 1977, pp. 28–29. Oceans Society of Australia, Melbourne.
- CRAWFORD I M 1977. Legislation–Maritime archaeology legislation in Western Australia. In: Green J N (ed.) Papers First Southern Hemisphere Conference on Maritime Archaeology, Perth, Western Australia, 1977, pp. 30–32. Oceans Society of Australia, Melbourne.
- Drake-Brockman H 1963. Voyage to disaster. Angus & Robertson, Sydney.
- EDWARDS H 1966. Islands of angry ghosts. Angus & Robertson, Sydney.
- EDWARDS H 1970. The wreck on Half Moon Reef. Rigby Limited, Adelaide.
- GREEN J N 1977a. Australia's oldest wreck: the loss of the Trial 1622. British Archaeological Reports Supplementary Series 27.
- GREEN J N 1977b. The AVOC jacht Vergulde Draeck wrecked Western Australia 1656. British Archaeological Reports Supplementary Series 36.
- Green J N 1989. The loss of the Verenigde Oostindische Compagnie retourschip Batavia, Western Australia 1629: an excavation report and catalogue of artefacts. British Archaeological Reports International Series 489.
- GREEN J N (Editor) 2007. Report on the 2006 Western Australian Museum Department of Maritime Archaeology Cape Inscription National Heritage Listing Archaeological Survey.

- Australian National Centre of Excellence for Maritime Archaeology Special Publication 10.
- GREEN J N (Editor) 2011. Shipwrecks of the Ningaloo Reef: Maritime Archaeological Projects from 1978–2009. Australian National Centre of Excellence for Maritime Archaeology Special Publication 15.
- GREEN J N, GAINSFORD M & STANBURY M 2004. Department of Maritime Archaeology, Western Australian Museum, A Compendium of Projects, Programmes and Publications 1971–2003. Australian National Centre of Excellence for Maritime Archaeology Special Publication 9.
- HENDERSON G 1980. *Unfinished voyages. Western Australian shipwrecks* 1622–1850. University of Western Australia Press, Nedlands.
- Henderson G 1986. Maritime archaeology in Australia. University of Australia Press, Nedlands.
- Henderson G & Henderson K-J 1988. Unfinished voyages. Western Australian shipwrecks 1851-1880. University of Western Australia Press, Nedlands.
- Kennedy G A 1998. Protection of sites and ANCODS. *In:* Green J N, Stanbury M & Gaastra F (eds) *The ANCODS Colloquium*, pp. 30–36. Australian National Centre of Excellence for Maritime Archaeology Special Publication 3.
- McCarthy M (Editor) 1988. Iron ships & steam shipwrecks: papers from the first Australian seminar on the management of iron vessels & steam shipwrecks. Western Australian Museum, Perth.
- McCarthy M (Editor) 2013. Shipwrecks of Australia's West Coast. Western Australian Museum, Perth.
- Pendal P G 1994. Select Committee on Ancient Shipwrecks, Report Presented by Hon. P.G. Pendal, MLA Laid on the Table of the Legislative Assembly on 17 August 1994. W.A. Legislative Assembly, Perth.
- PLAYFORD P E 1996. Carpet of silver, the wreck of the Zuytdorp: University of Western Australia Press, Nedlands.
- ROBINSON D 1977. Amateur maritime archaeology: the role of the amateur in maritime archaeology. In: Green J N (ed.) Papers First Southern Hemisphere Conference on Maritime Archaeology, Perth, Western Australia, 1977, pp. 110–112. Oceans Society of Australia, Melbourne.
- Western Australian Consolidated Acts 2010. http://www.austlii.edu.au/au/legis/wa/consol_act/maa1973200/>.
- WORSLEY J, WORSLEY P & GREEN J N 2012. Capes of Sunset Western Australia's Maritime Heritage between the Peel Inlet and Flinders Bay. Australian National Centre of Excellence for Maritime Archaeology Special Publication 13.
- Worsley J, Worsley P, Totty D & Green J N 2008. A Windswept Coast Western Australia's Maritime Heritage between the Moore River and the Zuytdorp Cliffs. Australian National Centre of Excellence for Maritime Archaeology Special Publication 11.

Received 3 October 2013; accepted 16 October 2013



Vegetation survey in Western Australia

N GIBSON

Science Division, Department of Parks and Wildlife, Locked Bag 104, Bentley Delivery Centre, WA 6983, Australia meil.gibson@dpaw.wa.gov.au

Ludwig Diels (1906), Charles Gardner (1928, 1956) and John Beard (1980, 1981) in turn produced increasingly more detailed biogeographical classifications and vegetation maps for Western Australia. These three men are largely responsible for our current understanding of the broad-scale patterning of vegetation across the State and, while John Beard's contribution to vegetation mapping has long been recognised, Gardner's earlier state-wide vegetation map has generally been attributed to other authors. Since Beard's final map was produced in 1981 there has been no consistent program to map the vegetation of Western Australia at a higher resolution. What such a program might entail and what impediments need to be overcome are reviewed.

KEYWORDS: Beard, biogeography, Diels, Gardner, mapping, survey, vegetation.

INTRODUCTION

The task of basic inventory of the plant species of Western Australia from a European perspective had begun in the late 1600s by Vlamingh (in 1696/97) and Dampier (in 1699) and was continued by Brown (visited 1802), Drummond (active mid 1830-1851), Preiss (visited 1838-1842), Diels and Pritzel (visited 1900-1901), Gardner (active 1920-1969) and continues to this day with the State collection now numbering over 730 000 specimens (Hopper 2003, 2004; Underwood 2011). In contrast, the broad-scale survey of vegetation of Western Australia only began in earnest in the opening years of the 20th century (Diels 1906) and culminated toward the end of that century as a series of detailed vegetation maps covering the whole State with a second more detailed series covering the southwest (Beard 1981). It was in essence the work of three remarkable men: Ludwig Diels, Charles Gardner and John Beard. Since that time further mapping at a variety of scales and for a variety of purposes has been undertaken (Havel & Mattiske 1999; van Vreeswyk et al. 2004; Craig et al. 2008; Sandiford & Barrett 2010) as have quadrat-based biological surveys (Keighery et al. 2007). All of this later work builds to a greater or lesser degree on Beard's broad-scale vegetation mapping.

Diels, Gardner and Beard all had strong connections with the Royal Society of Western Australia and its precursors with Gardner and Beard serving terms as President of the Society (1941-42 and 1986-87) and as recipients of the Society's Medal in 1949 and 1983, respectively. While the history of Beard's Vegetation Survey of Western Australia project and his collaboration with the Geography Department of the University of Western Australia is well documented (Beard & Webb 1974; Beard 1979; Beard et al. 2013) less is known of the contributions of Diels and Gardner.

LUDWIG DIELS

Ludwig Diels was just 26 years old when he came to Western Australia with his friend Ernst Pritzel to study

the flora and vegetation of Western Australia in October 1900. After their arrival in Albany they quickly made their way to Perth where they rented premises at 194 Roe Street which they retained for their 14 month stay. Diels had various letters of introduction to the Premier Sir John Forrest including one from Edward Wittenoom the Agent General in London urging Forrest to facilitate Diels' work and to introduce him to Mr Bickford then President of the Mueller Botanical Society (SROWA 1900). Diels wasted little time on his arrival in Perth writing to Forrest on the 6 November 1900 requesting permission to 'collect wild plants everywhere right over the colony' and to be issued two 12 month tickets for the Government Railway Lines. In return Diels offered to present duplicate specimens of all their collections to the Government along with copies of their subsequent publications (SROWA 1900). These requests were received favourably and rail passes were subsequently issued and utilised on most of their collection trips (Diels 1906; Beard 2001a figure 2; Beard & Kilian 2003).

As well as undertaking an exhaustive field program, they also were quite active in the Mueller Botanical Society attending meetings and flower shows throughout the year (West Australian 1901c). In November 1901, close to the end of their stay, Diels gave a lecture to the Society on *Plant forms and climate in Western Australia* (Diels 1902) and both young men were heartily complimented on their endeavours at the last meeting they attended in December 1901 just prior to their departure (West Australian 1901d).

Their expedition to Western Australia must rank as one of the most productive and timely undertaken in Western Australia. Diels collected some 4660 specimens while Pritzel collected multiple sheets of some 1016 collections (Diels & Pritzel 1904-05) as well as jointly collecting a set that was donated to the Perth Museum during their stay (West Australian 1901a, b). These collections formed the basis of their taxonomic and biogeographical studies. By 1906 two significant volumes had been published. The first was a taxonomic treatise Fragmenta Phytographiae Australiae occidentalis (Diels & Pritzel 1904-05) naming ~300 new taxa of which just over half are currently accepted. The second volume published in 1906 was the first detailed biogeographic

© Crown Copyright

treatment of the Western Australian flora and vegetation. It was titled *Die Pflanzenwelt von West-Australien südlich des Wendekreises* (Diels 1906) and in this 400 page tome Diels defined two botanical provinces in southern Western Australia: the Eremacan Province covering the arid interior, which he subdivided into two botanical districts; and the Southwest Province, which he subdivided into six botanical districts.

Diels' concepts of the major biogeographical patterns (Diels & Pritzel 1904-05; Diels 1906) although later modified by Gardner & Bennetts (1956), Beard (1980) and others (Thackway & Cresswell 1995) formed the foundation for our current understanding of the biogeography of the flora of southern Western Australia. The 1906 treatise also included the first vegetation map of Australia as a coloured plate at 1: 27 000 000 scale and, as Beard (2001b) pointed out, the map and the associated table appears to be incongruent with the detailed description of the Western Australian vegetation in the later chapters. Nonetheless it is a remarkably accurate representation of broad vegetation patterns considering the scale and time it was produced.

Until recently there has been little direct information as to the sources used to compile this map. Diels' diaries have not been located and were probably lost when the Berlin herbarium was bombed toward the end of the Second World War. The recent rediscovery of two albums of Pritzel's photographs in Berlin from which their itinerary after leaving Western Australia can be deduced (Beard & Kilian 2003) and the acknowledgements in the Fragmenta suggests several possible sources. Diels and Pritzel travelled extensively in eastern Australia in the first half of 1902, they are likely to have met L Rodway in Hobart (January 1902), G Luehmann in Melbourne (March), J H Maiden in Sydney (April) and F M Bailey in Brisbane (May) on their way back to Europe. These people or others they met at the State Herbaria of Victoria, New South Wales and Queensland are likely to have been his primary sources.

CHARLES GARDNER

Charles Gardner held the position as Government Botanist and head of the herbarium from 1929 until 1960 having worked previously in the Forest Department (1920–1924) (Green 1990). He is primarily remembered as a taxonomist (having described 10 genera and over 260 taxa, and provided new combinations for a further 57 taxa) and plant collector (with over 20000 specimens in the Western Australian Herbarium –PERTH) but he also made a significant contribution to biogeography and vegetation mapping.

It is seldom recognised that Gardner produced the first vegetation map of the State at 1:3 125 000 scale in 1928 (Gardner 1928 appended to Kesssell 1928). This map shows nine major vegetation types (seven forests/woodlands and two treeless types) and alludes to two further units too small to map. This map is usually ascribed to Jutson (1914) but in fact only appeared in the second and third editions of that work (Jutson 1934, 1950). The 1928 map gives 'Compiled by C.A. Gardner' and 'S.L. Kessell, Conservator of Forests. January, 1928' separately; indicating it was published with Kessell's

report on forest resources in Western Australia. Contemporary newspaper reports confirm that this was Gardner's map (West Australian 1928; Daily News 1928): interestingly Kessell gives no acknowledgement to Gardner despite using the map as a basis for discussion in his report. Gardner's map was republished in 1952 and 1967 on less-detailed base maps. The 1952 edition attributes the map to Gardner in association with T N Stoate, and separately acknowledges Gardner for providing the added information on eucalypt distributions (absent on the 1928 map) (Gardner & Stoate 1952). The authorship of the 1967 map is attributed to A C Harris but again acknowledges Gardner for additional eucalypt information (Harris 1967). Both Stoate and Harris were the Conservator of Forests (i.e. head of the Forest Department of Western Australia) at the time the maps were produced. All three versions of the map were published by the Forest Department.

Gardner appears to have largely relied on his own knowledge of the vegetation of Western Australia in the compilation of this map. The newspaper report that marked the release of the map stated 'That it has been prepared with such accuracy is due to the extensive local travels of the compiler, who has personal knowledge of all the areas marked, with the exception of the deserts' and 'In defining the limits of this desert, it was necessary to rely for the most part upon the journals and diaries of explorers' (West Australian 1928). As Gardner never collected across the eastern half of the State, except for the Kimberley (Figure 1), this appears to be somewhat of an exaggeration. The 1928 base map certainly showed many of the explorer's routes and Gardner must have made more use of their journals than the article suggested. In addition the depiction of the extent of the southwest forest on Gardner's map appears to be based, in part, on contemporary and earlier Forest Department mapping of these areas (Kessell 1928; Moore 1902).

Gardner had been working on a vegetation map for some years and he produced his first State-wide map in 1921 (Daily News 1928) but no extant copy of that earlier map is known. An interesting aspect of Gardner's map, which shows parallels with Diels' map, is the depiction of a narrow belt of 'Savannah forest and woodlands' to the east of the 'Sclerophyll forest' (jarrah) occurring in a mosaic with his other temperate woodland type. On Gardner's larger scale map this unit also becomes the dominant vegetation unit on the Swan Coastal Plain to the west of the jarrah forest, and along the south coast. His legend defines the savannah woodland as eucalyptdominated forests and woodlands with a herbaceous undergrowth, primarily grasses. This map unit also covers extensive areas of the tropical north.

On Diels' map there is a savannah woodland/forest unit ('savannen-wald') in a similar location to the east of the jarrah forest in a mosaic with a mallee scrub and sand heath unit. Diels also used this mapping unit to encompass the widespread temperate grassy woodlands of eastern Australia and the tropical savannahs of the north.

Currently true savannah woodlands (i.e. woodlands with grass-dominated understorey) are very rare in southwest Western Australia and Beard (2001b) considered Diels' use of the term encompassed young green herbage which could consist of annuals of all kinds

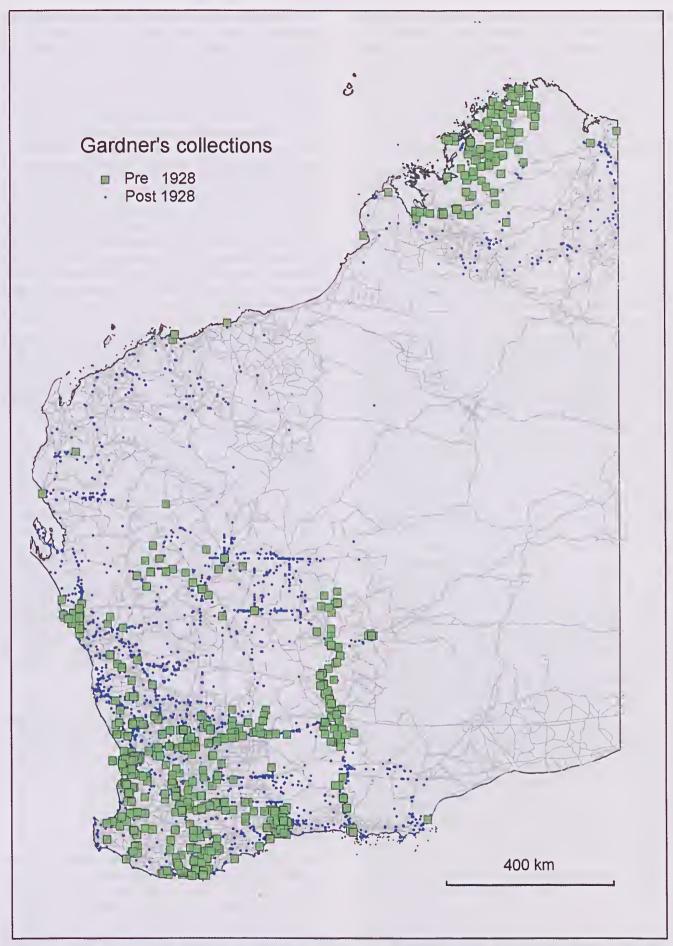


Figure 1 Gardner's Western Australian collections held in PERTH: squares indicate collections made before the publication of his vegetation map in 1928, circles indicate subsequent collections.

and the new shoots of perennials such as sedges, rushes as well as grasses. This interpretation is supported by Diels' (1906) comment on the vegetation of the southwest where he states that: 'The rarity of occurrence of members of the Graminaceae and Compositae in the southwest Australia is very difficult to understand. Climatically similar areas are rich in members of both these families. Moreover introduced species of both, particularly annuals, do remarkably well in south-west Australia. Briza maxima, for example, is at present more common than any of the indigenous grasses.'

Gardner's (1928) use of the term 'savannah' in southwestern Australia must also be considered to be somewhat imprecise. In a very small-scale vegetation map of the State included in his Presidential Address (Gardner 1944) he separated this southwestern savannah unit which he calls 'Savannah (temperate) Woodland' and somewhat modifies its boundaries. In his discussion of this formation he describes woodlands of Encalyptus wandoo (sensus lat.), Acacia acuminata and Encalyptus loxophleba with a low shrubby or herbaceous undergrowth, 'forming open savannah like country'.

Similarly on the Coastal Plain he describes the Tuart forest 'as a type of savannalı forestwitlı an understory of Agonis and Banksia, Melaleuca and Hakea, with a herbaceous ground layer where shrubs are comparatively few'. Given Diels comments it seems unlikely that either of these vegetation types had understorey dominated by grasses, except perhaps for short periods immediately after fire or in very specific habitats. Gardner (and Diels before him) appear to be using the term savannah to describe the open nature of the canopy species and the lack of a dense shrub layer in the understory. No unequivocal evidence such as a painting or early photograph that depict communities dominated by grasses are known from these areas.

Gardner did not include any biogeographical information on his 1928 map or the later reprints. His notion of the biogeographic regions developed over a number of decades. He would have had the opportunity of discussing them with Diels as he visited Berlin (where Diels was Director) during the time he spent as the first Australian Botanical Liaison Officer based in Kew (1937-39: Marchant 1996). About this time he was collaborating with Teakle to publish a map (1: 9 580 000) showing soil zones subdivided into soil and ecological regions (Teakle 1938). This map depicts several soils/ecological regions in northern and eastern Western Australia (Hann, Fitzroy, Ashburton, Carnegie) that Gardner would go on formally to describe as botanical districts (with amended boundaries) in his 1956 publication (Gardner & Bennetts 1956). In his 1942 Presidential address to the Royal Society of Western Australia he provided a detailed analysis of the vegetation across the State in relation to climate and soils (Gardner 1944). Here he extended Diels' biogeographical classification to include a third botanical province covering the Kimberley and Pilbara and described three major formations occurring there (his plates IX and X). The small map (1:15 840 000) showing the boundaries of all three provinces clearly demonstrates the connection with broad-scale climatic factors (plate IX). His boundary between the Southwest and Eremaean Provinces appears significantly further inland than Diels' boundary.

In the south of the State the boundaries of the major vegetation formations are largely the same as his 1928 map except that the boundary between 'Mulga bnsh' and 'Sclerophyll woodland' was moved to the southwest in the section from Shark Bay to Lake Moore. In the north the boundaries of the 'Tropical sclerophyll woodland', 'Monsoon woodland, savannah woodland and riverine forest' and 'Desert' formations remain essentially the same, however the classification and boundaries of the 'Savannah and open savannah woodland' and 'Triodia steppe' have changed considerably. Gardner collected in the Pilbara after 1928 but what further information he gathered to inform these changes in the eastern Eremaean is not clear (Figure 1).

Gardner formally described his botanical provinces and districts and provided a map (1:13 400 000) as an appendix in Gardner & Bennetts' (1956) *The Toxic Plants of Western Australia*. The boundary of the Southwest Province move slightly further inland while the boundary of the Northern Province was largely consistent with his 1942 boundary except for northeast contraction between the Ashburton and Fortescue Rivers. He described five districts in the Northern Province, five in the Eremaean and six in the Southwest Province. In both the Eremaean and Southwest Provinces he retained the districts described by Diels but redefined their boundaries. This classification was to stand for almost 40 years until the completion of Beard's seminal mapping program (Beard 1980).

While Gardner's classification was the most widely applied, further research into biogeographic patterns in Western Australia continued, notably the work of Nathanial Speck (Gibson et al. 1997) and Nancy Burbidge (1960). As part of his PhD work Speck (1958) mapped structural vegetation units across the southwest and undertook a biogeographical analysis of the species distributions patterns in the Proteaceae. From the mapping he recognised 62 vegetation communities in 26 vegetation systems. Based on both these datasets he proposed modifications to Diels' phytogeographic districts including the addition of a Lesueur botanical district and the splitting the southern sandplains into two districts to better reflect centres of species richness. Unfortunately this work was never formally published, and has largely been ignored (but see Lamont & Connell 1996).

The other major contribution during this period was the continental-scale phytogeographic analysis published by Burbidge (1960). In this classification the intermediate nature of the flora and vegetation of the southwest interzone, occurring between the species rich southwest and the more arid interior, was identified for the first time.

JOHN BEARD

Beard has outlined the general methods he use in the *Vegetation Survey of Western Australia* to produce the twenty 1:250 000 maps of the southwest and the seven 1:1 000 000 sheets mapping the vegetation across the whole state (Beard & Webb 1974; Beard 1979, 1981; Beard *et al.* 2013). This monumental undertaking was supported by the Geography Department at the University of Western Australia with some initial assistance from

Kings Park Board with Australian Biological Resources Study (Beard 1979) as well as considerable assistance from the Western Australian Herbarium and from Pauline Fairall, an honorary botanist based at Kings Park. The level of available resources profoundly affected both the scale of the mapping and the classification system adopted (Beard & Webb 1974; Beard 1979). What made the project feasible was the availability of aerial photography mosaics across the much of the State for the first time (Beard 1979).

The first field work began in August 1963 and ran until April 1978 with the final map being produced in 1981. Beard kept a series of collection books, field log books and a 1:3 168 000 scale map of the routes he traversed throughout the survey; he donated these to the Western Australian Herbarium library in December 2002 (Figure 2). For each trip his log books provide a record of running observations tied to the distance from known positions; these were subsequently used in the revision of the initial air photo interpretation (Beard & Webb 1974).

Beard normally collected extensively on each of his trips. His collection numbers for the survey ran from 2556 (August 1963) to 8212 (14 April 1978), some 72% (4072) of which are currently lodged in PERTH. Significant assistance was provided by the Western Australian Herbarium and by Fairall in the identification of these collections. Three field trips were undertaken with a botanist from the herbarium (two by Alex George and one by Paul Wilson) who undertook the bulk of the collecting on these trips (Figure 2). According to his log books regular field assistance was also provided by Fred Lullfitz, Pamela Beard, Ernie and Magada Wittwer, Arthur and Pauline Fairall and Herbert Demarz, amongst others.

In addition to publishing the two series of vegetation maps, Beard (1980) also published a new phytogeographic map of Western Australia at 1:2 500 000 and a coloured vegetation map of the whole State at 1:3 000 000 (Beard 1981). This map was further reduced and simplified and has appeared (at 1:10 000 000 scale) in a number of publications including Beard's *Plant Life in Western Australia* (Beard 1990).

Table 1 List of Beard's trip log books showing the period and distance covered.

Book	Period	Distance (km)
1	Aug 1963–Jan 1965	19 062
2	Sept 1963-Oct 1966	18 323
3	May 1965–Sept 1967	17 848
4	July 1967-Sept 1968	23 630
5	Aug 1968-Sept 1970	15 097
6	Sept 1973-Nov 1974	15 414
7	May 1974-Sept 1976	17 512
8	Sept 1976-April 1978	8 635
Total	•	135 523

Books are held in the library archive of the Western Australian Herbarium.

Beard's vegetation maps, based on 17 years of field work using the available air photo mosaics, provide much more detail information on vegetation patterning compared to the earlier work. At the larger 1:1 000 000 scale Beard recognised 130 vegetation units (Beard & Sprenger 1984) which were amalgamated into 50 units at the smaller 1:3 000 000 scale: this can be compared to the nine units recognised by Gardner at a similar scale.

Beard's original 1:250 000 base maps have recently been digitised and updated and a new digital 1:3 000 000 scale vegetation map has been published (Beard *et al.* 2013). The new edition recognises 70 map units (50 vegetation units and 20 mosaic units), compared with the 50 map units in the first edition. This more detailed classification is based on almost 900 mapped associations covering close to 30 000 polygons: for details of the methodology see Beard *et al.* (2013).

Beard's mapping provided for the first time the ability to accurately locate major changes in vegetation associations. This led to the publication of Beard's phytogeographic map which provided a far more detailed biogeographic classification than the earlier classifications of Diels and Gardner. For the first time the boundaries of the three botanical provinces, the twenty botanical districts and the interzone (which had been previously recognised by Burbidge) were available at a useable scale (Beard 1980). Beard's Northern Province and its four botanical districts had radically different boundaries to those of Gardner, most notably in excluding the Pilbara region. His Eremaean Province encompassed 11 botanical districts (cf. five of Gardner) and the Coolgardie Interzone, while the Southwest Province was made up of four botanical districts with the forested district (Darling) being subdivided into four subdistricts. A small-scale map of this classification was later published with slightly revised nomenclature (Beard & Sprenger 1984; Beard 1990).

At about the same time as Beard published his phytogeographic map Takhtajan published a review of the classification of the floristic regions of the world largely based on occurrence of endemic taxa at different taxonomic levels. He recognised six plant kingdoms containing 35 regions which were further subdivided into a series of one or more botanical provinces. This classification first appeared in Russian in 1978 followed by an English translation (Takhtajan 1986).

Takhtajan considered that the three provinces recognised by Beard should be classified as regions indicating a higher level of floristically significance than previously recognised in a global context. Cox (2001) in a worldwide review of biogeographical regions supported Takhtajan's decision. Following on from earlier work (Hopper 1979) Hopper & Gioia (2004) published a map of the Southwest Australian Floristic Region based on species richness and endemism subdivided into three provinces and 11 districts which incorporated some of the elements of Speck's (1958) classification. Subsequently there has been wide general acceptance of the recognition of the southwest as a botanical region and in the utility of their provinces in analysis in both phylogenetic (Cooper et al. 2011; Cardillo & Pratt 2013) and ecological studies (Gibson et al. 2012; Merwin et al. 2012). Their concepts of botanical districts are yet to be rigorously tested.

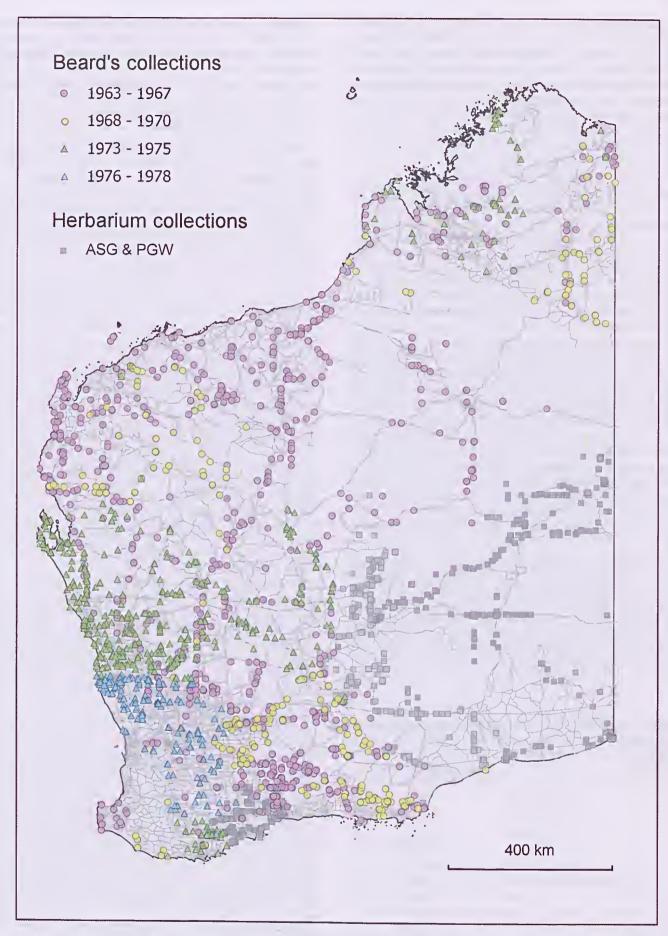


Figure 2 Beard's collections 1963–1978 held in PERTH made during the Vegetation Survey of Western Australia and the collections made by two PERTH botanists (Alex George and Paul Wilson) who accompanied him on three of his expeditions.

Notwithstanding this more recent work Beard's (1980) classification still forms the basis of current biogeographic regionalisation used by the State and Federal governments as a conservation planning tool [Thackway & Cresswell 1995: an Interim Biogeographic Regionalisation for Australia (IBRA)]. The latest IBRA version recognises an additional interzone to the northwest of the Coolgardie Interzone running up to Shark Bay, a further two bioregions (equalivent to Beard's districts) in the Eremaean Province and the seven bioregions in the Southwest Province modifying Beard's original hierarchical scheme.

A recent survey of the terrestrial biota across the southwest covering six IBRA bioregions provided little support for the utility of this classification either in terms of species composition of the vegetation (Gibson *et al.* 2004) or the biota as a whole (McKenzie *et al.* 2004). In addition IBRA does not recognise the hierarchal nature of Beard and later classifications and this can lead to highly inaccurate assessments of the regional and global significance of individual bioregions. A serious reappraisal of the effectiveness of the IBRA as a conservation planning tool is overdue.

STATE-WIDE MAPPING POST-BEARD

The major uses of vegetation mapping are to: (i) document the diversity of plant cover across a region; (ii) reflect the current knowledge of the structure and biogeographic patterns of the vegetation; and (iii) determine a baseline for land managers (Mucina *et al.* 2006). In land management vegetation mapping is used in both the assessment of conservation status and in the assessment of environment impacts. It is also used in the identification of potential land uses and as a surrogate for fuel loads in fire-management planning, and as planning units in local and regional management plans. A vegetation map is nonetheless a model of vegetation patterning and the success of a vegetation map to fulfill these various roles is dependent on the scale and classification used in the mapping.

Broad-scale mapping such as Beard's can be considered a 'coarse-filter approach' (Noss 1987, 1990) and has been used as a surrogate for biodiversity patterning at the Commonwealth level (Thackway & Creswell 1995) and for initial conservation assessments at the State level (Brandis & Mitchell 2000; May & McKenzie 2003). However it appears to be, at best, only moderately accurate in predicting patterns in floristic composition in the Southwest and the ranges of the Eremaean (Hnantiuk & Hopkins 1981; Burgman 1988; Gibson *et al.* 1994, 2004, 2012). Accurate identification of these patterns requires a more 'fine-filter approach'.

Beard (1979, 1981) clearly realised the implications of scale and classification method he chose and he deliberately used a 'coarse-filter approach' to enable him to map the vast area of Western Australia in 15 year period with limited resources. The mapping was therefore at the plant association (defined dominant species or group of closely related species) or plant formation (structural) level. He did not have time to use quantitative floristic analyses or phytosociological approaches (i.e. quadrat/révélée-based methods

capturing compositional data) but expected more detailed mapping/classification work would be undertaken at a later stage using his *Vegetation Survey of Western Australia* as a framework (Beard 1981). This is exemplified by Muir's (1977) subsequent fine-scale mapping of wheatbelt reserves where he modified Beard's classification to better reflect both vegetation pattern and animal habitats. Muir's classification has subsequently been widely used in the southwest.

However, many other projects that have mapped smaller regions of the State for specific purposes show little correspondence to Beard's classification framework. Such mapping includes: land systems mapping of the pastoral region (van Vreeswyk *et al.* 2004 and earlier surveys at 1:250 000); vegetation complexes in the southern forests (Havel & Mattiske 1999 at 1:500 000); vegetation types in regional planning areas (Sandiford & Barrett 2010 at 1:25 000); or specific locations (Craig *et al.* 2008 at 1:10 000) and other ongoing large-scale mapping related to resource development proposals. Because of the different methods and/or scales used they depict quite different facets of the vegetation pattern.

The question arises could the Beard's Vegetation Survey of Western Australia be extended to provide consistent high-resolution vegetation mapping across the whole State that could be used for a variety of land planning and land management purposes? Or, alternatively, is the future the continuation of the multitude of smaller projects each designed to answer specific questions but contributing little in the development of a consistent State-wide perspective.

There are several issues involved with developing a high-resolution State-wide vegetation coverage and these are discussed below.

Ouestions of scale

Since the production of Beard's maps there has been an increasing requirement for higher resolution coverage to aid in land-management decisions (Salt *et al.* 2008). Current mapping for land planning and environmental impact is generally undertaken at scales of between 1:10 000 and 1:50 000. For example, recent mapping of 10 200 ha in the Ravensthorpe Range at scale of 1:10 000 identified 70 vegetation units with a mean polygons size of 1.4 ha (Craig *et al.* 2008). In contrast Beard mapped six vegetation units in the same area.

Clearly it would not be possible to undertake mapping at this level of detail across the whole State, even mapping the State at 1:100 000 would require over 1000 map sheets. It could be argued however that given the geographic information systems (GIS) now available it is not necessary to work to a single map scale. In large sections of the Eremaean where there is high degree of both geomorphological and vegetation uniformity such high-resolution mapping would not be required to aid land-planning decisions. High-resolution mapping could be concentrated in areas where it is most need for conservation or other type of land-use planning.

Types of classification

The classification used to denote vegetation units also has a profound effect on the final vegetation map no matter what the scale. In southwestern Western Australia as in southern Africa there is often little or no relationship between units based on vegetation structural and units based on species composition (Hnantiuk & Hopkins 1981; Burgman 1988; Gibson et al. 1994, 2004, 2012; Rebelo et al. 2006). This is a major issue in areas of high species turnover but relatively uniform vegetation structure. As most mapping relies on interpretation of air photo or satellite imagery to identify the initial mapping units there is a strong structural bias in these classifications. In southern Africa a workable classification (at 1:250 000) has been developed incorporating addition information on substrate and geographical area but a method that directly includes detailed compositional information is still lacking (Rebelo et al. 2006).

In recent years more sophisticated approaches to vegetation mapping have been used that incorporate modelling vegetation units using plot data and ancillary environmental information (Ferrier et al. 2002; Keith 2004; Accad & Neil 2006). In addition the launch of hyperspectral satellites in the near future will fundamentally change the way vegetation mapping is undertaken, opening the possibility of incorporating compositional information (based on spectral reflectance) for the first time in areas of continuous vegetation cover (Schmidtlein & Sassin 2004). In more arid areas with low vegetation cover this technology will be able to map substrate chemistry in considerable detail (van der Meer et al.2012) that could then be incorporated into the vegetation mapping. In addition the increasing availability of LIDAR data allows detailed structural information to be captured (Hall et al. 2009). If such techniques can be fully developed and integrated, then high-resolution vegetation mapping of large areas could be undertaken at reasonable cost.

Consistency of methods

Most current vegetation mapping is being undertaken for the resource industry for development applications. This mapping is generally very detailed but over relatively small areas. There is currently no consistent methodology used in the mapping and published details of method used are generally scant. If a State-wide mapping program was to be implemented to gather data from all available sources then a detail standard methodology would need to be developed along with quality assurance protocols to ensure consistent data quality that would allow highresolution map products to be produced.

Mapping as a model

All vegetation mapping is a model of the change of vegetation units across the landscape. What is often lacking in vegetation mapping is some measure of the homogeneity of the mapped units. This could be particularly important if vegetation in different areas is mapped by different groups. Such mapping should also be subject to strict accuracy assessment that is published with the maps. This will require both the collection of sufficient plot-based data to allow the level of heterogeneity within mapping units to be determined, and the lodgement of voucher specimens to ensure the continued utility of these data through time. This implies that an ongoing vegetation mapping program would need to be supported by vegetation information system

to capture both plot and voucher data in a consistent, transparent and repeatable way (Salt et al. 2008).

While Beard did not have the resources to establish permanent plots in his mapping units he did recognise the need to have a consistent taxonomy and collected over 4000 voucher specimens, a practice rarely seen in current vegetation mapping programs.

Possible future directions

A number of resources would need to available to develop integrated high-resolution vegetation coverage across the State, these include:

- (1) Commitment of Government, Government Agencies and Resource Industry to the development of such a map.
- (2) Identification of priority areas for mapping. This will be areas where there is the most pressing need for high-resolution mapping: these are likely to include the Swan Coastal Plain, and mining areas of the Midwest, Goldfields and Pilbara.
- (3) A core mapping group to be established with ongoing funding. This group would: (i) develop the mapping standards; (ii) established the infrastructure for a vegetation information system, (iii) be responsible for the ongoing maintenance of the vegetation information system including databases, GIS capacity, and web-based applications for easy access to data; (iv) provide the quality assurance oversight of data being contributed to the system including accuracy assessments of contributed mapping products; (v) provide access to all contributed mapping products both in digital and hard copy forms; and (vi) develop the capacity for modelling of remote sensing data for use in vegetation mapping.

The next generation of vegetation maps will not be able to be provided by a single person as the task is now far too complex at the scale required across an area as vast as Western Australia. It will nonetheless be built on the foundations established across the 20 century by Diels, Gardner and Beard.

ACKNOWLEDGEMENTS

Martyn Webb provided valuable insights into the early days of the Vegetation Survey of Western Australia and the collaboration between his department (Geography Department, UWA) and John Beard. I would also like to thank Steve Hopper for his constructive comments on an earlier draft of the manuscript.

REFERENCES

Accad A & Neil D T 2006. Modelling pre-clearing vegetation distribution using GIS-intergrated statistical, ecological and data models: a case study from the wet tropics of Northeastern Australia. *Ecological Modelling* 198, 85–100.

Beard J S 1979. Vegetation mapping in Western Australia. Journal of the Royal Society of Western Australia 62, 75–82.

Beard J S 1980. A new phytogeographic map of Western Australia. Western Australian Herbarium Research Notes 3, 37–58.

Beard J S 1981. Vegetation of Western Australia. 1: 3,000,000. Forest Department of Western Australia, Perth.

- Beard J S 1990. Plant Life of Western Australia. Kangaroo Press, Kenthurst.
- Beard J S 2001a. The botanists Diels and Pritzel in Western Australia: a centenary. *Journal of the Royal Society of Western Australia* 84, 143–148.
- Beard J S 2001b. A historic vegetation map of Australia. *Austral Ecology* 26, 441–443.
- Beard J S, Beeston G R, Harvey J M, Hopkins A J M & Shepherd D P 2013. The Vegetation of Western Australia at the 1:3,000,000 scale. Explanatory Memoir. (2nd edition). Conservation Science Western Australia 9, 1–152.
- Beard J S & Kilian N 2003. Diels and Pritzel in Eastern Australia: further information on their travels of 1902. Bulletin of the Ecological Society of Australia 33, 31–32.
- Beard J S & Sprenger B S 1984. Geographical Data from the Vegetation Survey of Western Australia. Vegetation Survey of Western Australia. Occasional Paper No. 2. Vegmap Publications, Applecross.
- Beard J S & Webb M J 1974. Vegetation Survey of Western Australia. 1:1 000 000 Series. Sheet 2. Great Sandy Desert. Map and Explanatory Notes. Part 1. The Vegetation Survey of Western Australia: its aims, objects and methods. University of Western Australia Press, Nedlands.
- Brandis A & Mitchell W 2000. Achieving a conservation reserve system in the Western Australian rangelands: a regional approach. *In: Proceedings of the Northern Grassy Landscapes Conference, Katherine, Northern Territory* 29-31 August 2000, pp. 112–116. Cooperative Research Centre for the sustainable development of tropical savannas, Casuarina.
- Burgman M 1988. Spatial analysis of vegetation patterns in southern Western Australia: implications for reserve design. Australian Journal of Ecology 13, 415–429.
- BURBIDGE N T 1960. The phytogeography of the Australian region. Australian Journal of Botany 8, 75-211.
- Cardillo M & Pratt R 2013. Evolution of a hotspot genus: geographic variation in speciation and extinction rates in *Banksia* (Proteaceae). *BMC Evolutionary Biology* **13**, 1–11.
- COOPER S J B, HARVEY M S, SAINT K M & MAIN B Y 2011. Deep phylogeographic structuring of populations of the trapdoor spider *Moggridgea tingle* (Migidae) from southwestern Australia: evidence for long-term refugia within refugia. *Molecular Ecology* 20, 3219–3236.
- Cox C B 2001. The biogeographic regions reconsidered. *Journal of Biogeography* 28, 511–523.
- CRAIG C F, HICKMAN E J, NEWELL J, McQUOID N, RICK A M & SANDIFORD E M 2008. Vegetation of the Ravensthorpe Range, Western Australia: Mt Short to Kundip 1:10,000 scale. Department of Environment & Conservation, and South Coast NRM Inc., Albany.
- Daily News 1928. Stupendous task. Classifying our flora. Botanist's big work. Published 3 March 1928, p. 5.
- Diels L 1902. Plant forms and climate of Western Australia. Journal of Proceedings of the Mueller Botanic Society 1(9), 4–14.
- Diels L 1906. Die Pflanzenwelt von West-Australien südlich des Wendekreises. Vegetation der Erde VII, Leipzig.
- Diels L & Pritzel E 1904-05. Fragmenta phytographiae Australiae occidentalis: Beitrage zur kenntnis der Pflanzen Westaustraliens, ihrer Verbreitung und ihrer Lebens-Verhaltnisse. Engelmann, Lepzig.
- Ferrier S, M, G & G 2002. Extended statistical approaches to modelling spatial pattern in biodiversity in northeast New South Wales. II Community level modelling. *Biodiversity and Conservation* 11, 2309–2338.
- GARDNER C A 1928. Vegetation map of Western Australia. Appended to: Forest Department Bulletin 42.
- Gardner C A 1944. The vegetation of Western Australia with special reference to climate and soils. *Journal of the Royal Society of Western Australia* 28, 11–87.

- GARDNER C A & BENNETTS H W 1956. The toxic plants of Western Australia. Western Australian Newspapers Ltd, Perth.
- GARDNER C A & STOATE T N 1952. Vegetation map of Western Australia (2nd edition). Forest Department of Western Australia, Perth.
- GIBSON N, KEIGHERY G J & KEIGHERY B J 1997. Contributions of N H Speck to the biogeography of Proteaceae in Western Australia. *Journal of the Royal Society of Western Australia* 80, 73–77.
- GIBSON N, KEIGHERY B, KEIGHERY G, BURBIDGE A & LYONS M 1994.

 A floristic survey of the southern Swan Coastal Plain. Report for the Australian Heritage Commission prepared by the Department of Conservation and Land Management, Perth.
- GIBSON N, KEIGHERY G J, LYONS M N & WEBB A 2004. Terrestrial flora and vegetation of the Western Australian Wheatbelt. Records of the Western Australian Museum Supplement 67, 139–189
- GIBSON N, MEISSNER R, MARKEY A S & THOMPSON W A 2012. Patterns of plant diversity in ironstone ranges in arid south western Australia. *Journal of Arid Environments* 77, 25–31.
- GREEN J W 1990. History of early Western Australian herbaria.
 In: Short P S (ed) History of systematic botany in Australia:
 Proceedings of a symposium held at University of Melbourne, 25-27 May 1988, pp. 23–28. Australian Systematic Botany Society, South Yarra.
- HALL R, WATKINS R, HEGGEM D, JONES K, KAUFMANN P, MOORE S B & GREGORY S J 2009. Quantifying structural physical habitat attributes using LIDAR and hyperspectral imagery. Environmental Monitoring and Assessment 159, 63–83.
- HARRIS A C 1967. Vegetation map of Western Australia (3rd edition). Forest Department of Western Australia, Perth.
- HAVEL J J & MATTISKE E M 1999. Regional Forests Agreement vegetation systems. 1: 500,000. Department of Conservation and Land Management, Como.
- HNATIUK R J & HOPKINS A J M 1981. An ecological analysis of kwongan vegetation south of Eneabba Western Australia. *Australian Journal of Ecology* 6, 423–438.
- HOPPER S D 1979. Biogeographical aspects of speciation in the south west Australian flora. *Annual Review of Ecology and Systematics* 10, 399–422.
- HOPPER S D 2003. South-western Australia, Cinderella of the world's temperate floristic regions 1. *Curtis's Botanical Magazine* 20, 101–126.
- HOPPER S D 2004. South-western Australia, Cinderella of the world's temperate floristic regions, 2. *Curtis's Botanical Magazine* 21, 132–180.
- HOPPER S D & GIOIA P 2004. The southwest Australian floristic region: evolution and conservation of a global hot spot of biodiversity. *Annual Review of Ecology, Evolution and Systematics* 35, 623–650.
- JUTSON J T 1914. An outline of the physiographical geology (physiography) of Western Australia. Geological Survey of Western Australia Bulletin 61.
- JUTSON J T 1934. The physiography (geomorphology) of Western Australia (2nd edition, revised). Geological Survey of Western Australia Bulletin 95.
- Jutson J T 1950. The physiography (geomorphology) of Western Australia (reprinted from the 2nd edition, with a revised geological map). Geological Survey of Western Australia Bulletin 95.
- Keighery G J, Gibson N, van Leeuwen S, Lyons N M & Patrick S 2007. Biological survey and setting priorities for flora conservation in Western Australia. *Australian Journal of Botany* 55, 308–315.
- KEITH D 2004. Ocean shores to desert dunes: native vegetation of New South Wales and the ACT. Department of Environment and Conservation, Hurstville.

- Kesssell S L 1928. Forestry and forest resources Western Australia. A statement prepared for the British Empire Forestry Conference Australia and New Zealand 1928. Forest Department Bulletin 42.
- LAMONT B B & CONNELL S W 1996. Biogeography of Banksia in southwestern Australia. *Journal of Biogeography* 23, 295–309.
- MARCHANT N G 1996. Gardner, Charles Austin (1896-1970).

 Australian Dictionary of Biography, Volume 14. Melbourne University Press, Melbourne.
- MAY J E & MCKENZIE N L 2003. A biodiversity audit of Western Australia's biogeographical subregions in 2002. Department of Conservation & Land Management, Kensington.
- McKenzie N L, Gibson N, Keighery G J & Rolfe J K 2004. Patterns in the biodiversity of terrestrial environments in the Western Australian Wheatbelt. Records of the Western Anstralian Museum Supplement 67, 293–335.
- MERWIN L, HE T & LAMONT B B 2012. Phylogenetic and phenotypic structure among *Bauksia* communities in southwestern Australia. *Journal of Biogeography* 39, 397–407.
- Moore N J 1902. Sketch map of part of South West Division of Western Australia showing approximate position of timber forests. In: Richardson G G Annual Report of the Woods and Forest Department for the Year Ending 1901. Government Printer, Perth.
- MUCINA L, RUTHERFORD M C & POWRIE L W 2006. The logic of the map: approaches and procedures. *Strelitzia* 19, 13–29.
- Muir B G 1977. Biological survey of the Western Australian wheatbelt. Part 2: Vegetation and habitat of Bendering Reserve. Records of the Western Australian Museum Supplement 3.
- Noss R F 1987. From plant communities to landscapes in conservation inventories: a look at the Nature Conservancy (USA) Biological Conservation 41, 11–37.
- Noss R F 1990. Indicators for measuring biodiversity: a hierarchical approach. *Conservation Biology* 4, 355–364.
- REBELO A G, BOUCHER C, HELME N, MUCINA L & RUTHERFORD M C 2006. Fynbos biomes. *Strelitzia* 19, 53–219.
- Salt C, Burrows N, Coates C & van Leeuwen S 2008. Vegetation Information Management System: the need for a new vegetation map of W.A. Vegetation Mapping Workshop 23-24 July 2008, Perth.
- Sandiford E M & Barrett S 2010. Albany regional vegetation survey: extent, type and status. Department of Environment and Conservation, Albany.

- Schmidtlein S & Sassin J 2004. Mapping of continuous floristic gradients in grasslands using hyperspectral imagery. *Remote Sensing of Environment* 92, 126–138.
- Speck N H 1958. The vegetation of the Darling-Irwin botanical districts and an investigation of the family Proteaceae in south Western Australia. PhD thesis, University of Western Australia, Perth (unpubl.).
- SROWA (STATE RECORDS OFFICE OF WESTERN AUSTRALIA) 1900. Dr Ludwig Diels. Visit to Western Australia to study flora of the colony, asking for railway passes etc. Item No. 1900/1598.
- Takhtajan A 1986. Floristic regions of the world (transl. T J Crovello & A Cronquist). University of California Press, Berkeley.
- Teakle L J H 1938. A regional classification of the soils of Western Australia. *Journal of the Royal Society of Western Australia* 24, 123–195.
- THACKWAY R & CRESSWELL I D 1995. An interim biogeographic regionalisation for Australia: a framework for setting priorities in the National Reserves System Cooperative Program. Version 4. Australian Nature Conservation Agency, Canberra.
- UNDERWOOD R 2011. A botanical journey: the story of the Western Australian Herbarium. Department of Environment and Conservation, Perth.
- VAN DER MEER F D, VAN DER WERFF H M A, VAN RUITENBEEK F J A, HECKER C A, BAKKER W H, NOOMEN M F, VAN DER MEIJDE M, CARRANZA E J M, DE SMETH J B, WOLDAI T 2012. Multi- and hyperspectral geologic remote sensing: a review. International Journal of Applied Earth Observation and Geoinformation 14, 112–128,
- VAN VREESWYK A M E, PAYNE A L, LEIGHTON K A & HENNIG P 2004. An inventory and condition survey of the Pilbara region, Western Australia. Department of Agriculture Technical Bulletin 92.
- West Australian 1901a. The Perth Museum. Recent additions. Published 18 April 1901, p. 7.
- WEST AUSTRALIAN 1901b. The Museum. July donations and purchases. Published 7 August 1901, p. 3.
- West Australian 1901c. News and Notes. Published 19 September 1901, p. 4.
- West Australian 1901d. News and Notes. Published 10 December 1901, p. 4.
- West Australian 1928. A vegetation map: State's plant geography. Published 29 February 1928, p. 7.

Received 18 June 2013; accepted 4 December 2013

Progress and prospects for understanding evolution and diversity in the southwest Australian flora

KR THIELE 1* & SM PROBER 2

- ¹Western Australian Herbarium, Department of Parks and Wildlife, Locked Bag 104, Bentley Delivery Centre, WA 6983, Australia.
- ² CSIRO Ecosystem Sciences, Underwood Avenue, Floreat, WA 6014, Australia.
- *Corresponding author M Kevin.Thiele@dpaw.wa.gov.au

The flora of southwest Australia has often been described as remarkable and special, both in an Australian and a global context, particularly because of its high species richness and endemism. Many explanations for the special characteristics of the region's flora have been proposed, most invoking a special evolutionary history. Relatively few studies, however, have explicitly compared either the floras or histories of southwest Australia and southeast Australia, a useful comparison as both may be assumed to have started with a similar flora and to have related histories. Such comparisons may be useful in discriminating the many factors, both historical and ahistorical, that may explain differences in richness and endemism. We analyse here flowering plant checklists from geographically comparable areas in southeastern and southwestern Australia to describe and quantify floristic differences, confirming that southwestern Australia has higher species richness but lower generic and family richness than southeastern Australia, and review previous explanations for these differences. We conclude that, while much has been achieved since Joseph Hooker first formally described these differences in 1859, much remains to be understood and knowledge gaps and paradoxes remain. Current explanations, while plausible, remain unproven, and differences in histories may or may not be the best explanations. Framing investigations of the special characteristics of southwestern Australia around null hypotheses may help provide a necessary rigour to such analyses.

KEYWORDS: biogeography, diversity, endemism, floristics, southeastern Australia, southwestern Australia.

INTRODUCTION

The flora of southwest Australia (SWA) is widely regarded as interesting and important at local, continental and global scales. Locally, many areas are rich and diverse, many species are naturally or anthropogenically rare or otherwise of conservation significance, and the flora provides an important and recognised character to SWA for the community and visitors alike. At a continental scale, SWA is one of 12 recognised centres of diversity and endemism in Australia (Crisp et al. 2002), while globally it is one of 25 designated global biodiversity hotspots (Myers et al. 2000) and one of 35 global floristic regions (Takhtajan 1986). Further, along with a small number of other temperate regions such as the Cape Floristic Region of South Africa (Manning & Goldblatt 2012) and California (Stebbins & Major 1965), the flora of SWA is unusually diverse for its latitudinal position, an outlier on a general global trend from high species richness in the tropics to lower richness polewards (Hillebrand 2004; Sniderman et al. 2013).

Joseph Hooker's seminal essay *On the flora of Australia, its origin, affinities and distribution* (Hooker 1859) provided an overview of the Australian flora as known at that time. Hooker was the first to formally describe special characteristics of the flora of SWA, particularly a 'remarkable' difference between the floras of southwestern and southeastern Australia (SEA) (although this had been prefigured in a letter from Robert

Brown to Joseph Banks in 1803, see Vallance et al. 2001). Noting first that SEA, with its greater area and productivity and more diverse topography, might be assumed to have a richer flora than SWA, Hooker concluded, following a careful enumeration and tabulation of all available data, that: (i) SWA was richer in species than SEA (3600 vs 3000 species); (ii) SWA had fewer genera and families than SEA (600/90 vs 700/125); (iii) there were more large genera (>10 species) in SWA than in SEA, and the largest genera in SWA had on average more species than the largest in SEA; (iv) most of the largest SWA genera were either small in SEA or did not occur there; (v) many of the extra genera in SEA had alliances outside Australia, while few SWA genera had such alliances (later restated as that the SWA flora was more characteristically 'Australian' than the SEA flora); (vi) SWA had a higher level of endemism than SEA; and (vii) SWA species tended to have narrower distributions than those in SEA

In correspondence to Darwin in the late 1850s, Hooker asserted that the SWA flora was 'the most extraordinary thing in the world' (Hopper & Lambers 2009). He regarded that the special character of SWA and the differences between the floras of SWA and SEA were globally remarkable and provided an important testing ground for 'whatever theory of creation and distribution may be established' (Hooker 1859 p. liii). He regretted that current theories of geology, biogeography and evolutionary history could not adequately explain it.

Diels (1906), following his own comparison between SWA and SEA and between these and the intervening eremaean zone, disagreed with Hooker. He focused

instead on the similarities between the two floras, noting that '[h]itherto there has always been the tendency to emphasize the differences and Hooker in particular stresses this' (Diels 1906 p. 322). He considered that the high degree of endemism in SWA, was 'over-rated', and disputed Hooker's emphasis on the global distinctiveness of the SWA–SEA comparison (Diels 1906 p. 39).

Subsequent to Diels, many authors retained a focus on the special characteristics of SWA, particularly with respect to species richness and endemism; these two special characteristics, and explanations for them, have dominated the literature. Many of the proposed explanations have been biogeographically narrative (sensu Ball 1976), and none have yet been adequately tested. Further, few attempts have been made since Hooker and Diels to rigorously compare the floras of SWA and SEA, to analyse the differences, and to reassess the conclusions they reached (Fox 1996). Most analyses of SWA's flora in recent years have either discussed features of the SWA flora without comparison with other areas, or have compared SWA with mediterranean-climate regions elsewhere in the world (Cowling et al. 1996; Cowling & Lamont 1998; Sauquet et al. 2009), or with other areas regarded as having a similar history (South Africa, the Venezuelan Pantepui Highlands: Hopper 2009). Fox (1996) noted that adequate modern comparisons between the floras of the SWA and SEA mediterranean-climate regions had not been made, while Sniderman et al. (2013) commented that comparisons between SWA and SEA may be more instructive than comparisons between SWA and mediterranean-climate regions elsewhere.

A number of recent authors have drawn attention to or described further special characteristics of the flora of SWA. Hopper et al. (1996 p. 8) considered that the environmental history of SWA has provided 'unparalleled opportunities for the persistence of relict terrestrial taxa'. Hopper & Gioia (2004) further noted the existence in SWA of a number of monotypic or small and phylogenetically isolated lineages, regarding this as special. Burbidge (1960) observed anecdotally that species in SWA tend on the whole to be distinct and comparatively uniform while many species in SEA are variable and less clear-cut, and attributed this to a possible greater incidence of hybridisation in SEA than SWA. Hopper (1994) concluded that hybridisation is less common in SWA than in SEA. However, Hopper & Gioia (2004) reviewed several genera where hybridisation is important and widespread in SWA; the situation is thus equivocal, and flora-wide comparisons have yet to be made.

Hooker based his conclusions regarding the unique and important characteristics of the SWA flora on an imperfect knowledge of the flora. Eight thousand Australian plant species were known at the time of his analysis and he was confident that the total Australian flora would not exceed a modest 9000–10,000 species; >24,000 species are known today (CHAH 2014). His knowledge of the flora of SWA and SEA was largely derived from a small number of collectors (Brown, Cunningham, Mitchell, Drummond, Preiss) and a handful of reports and descriptions of the flora (Brown 1810, 1814; Lehmann 1844–1848; Lindley 1838). As discussed by Diels (1906), his analyses were particularly hampered by substantial knowledge gaps regarding the eremaean flora that interposes between the two areas but

was included to some extent in both. Finally, the classification system for plants used by Hooker is now substantially out of date, having been improved in recent years by many rigorous phylogenetic and phytogeographic analyses.

Given that much more is now known about the floras of SWA and SEA and of Australia as a whole, and that web-based biodiversity aggregators such as Australia's Virtual Herbarium (http://avh.chah.org.au) and the Atlas of Living Australia (http://www.ala.org.au) greatly simplify analyses such as those performed (by hand) by Hooker and Diels, it is timely to repeat floristic comparisons between SWA with SEA and to revisit the special characteristics Hooker enumerated. This paper provides a modern reappraisal of Hooker's conclusions, assesses anew the characteristics (if any) of the flora of SWA that are special by comparison with elsewhere in Australia, and reviews current thinking around explanations of these special characteristics. It ends with a discussion of questions that remain at least partially unanswered, and an exploration of prospects for future progress in our understanding of the flora of the region.

IS SWA STILL SPECIAL, AND IF SO, IN WHAT WAYS?

While comparisons between geographic and taxonomic patterns of floristic richness and composition in Australia is easier today than in Hooker's time, definitional aspects of exactly what is meant by SWA and SEA have become more important; the paucity of knowledge available to Hooker made definitional questions almost irrelevant. SWA is, to a large extent, an ecological island (Carlquist 1974), readily definable as the Southwest Botanical Province of Diels (1906) and Beard (1990) or the largely equivalent South West Australian Floristic Region of Hopper & Gioia (2004). However, no such clearly defined region has been demarcated for SEA, where the environment of the temperate southeast is broadly contiguous with and grades into that of the east coast subtropics and tropics (Figure 1).

In order to compare regions with approximately equal areas, we define here SWA and SEA as follows. SWA (the South West Australian Floristic Region of Hopper & Gioia 2004) comprises the Geraldton Sandplains, Avon Wheatbelt, Swan Coastal Plain, Jarrah Forest, Warren, Mallee and Esperance Sandplain IBRA (Interim Biogeographic Regionalisation for Australia) bioregions (DEWHA 2008). SEA comprises the Victorian Midlands, Southern Volcanic Plain, South East Coastal Plain, South East Corner, South Eastern Highlands, Australian Alps, Sydney Basin and New South Wales South Western Slopes IBRA bioregions. This contiguous set of bioregions constitutes a relatively well-defined area of principally erosional land surfaces centred on the Great Dividing Range and bounded to the west and northwest by the alluvial-depositional plains of the Murray Darling Depression, Riverina and Cobar Peneplain, on the south by Bass Strait and to the north by subtropical coastal areas of northern New South Wales and the MacPherson-Macleay Overlap.

While the two regions as defined clearly differ in a number of respects, we regard that they nevertheless

Table 1 Geographic and floristic statistics for Southwest Australia (SWA) and Southeast Australia (SEA).

	SWA	SEA
Land area (km²)	302 627	321 110
Native species (endemic; % endemic)	6929 (3599; 51.9%)	4810 (659; 13.7%)
Native genera (endemic; % endemic)	698 (72; 10.3%)	916 (8; 0.9%)
Native families (endemic; % endemic)	122 (2; 1.6%)	162 (0; 0%)
Average species/genus	9.9	5.3
Average species/family	56.8	29.7
Average genera/family	5.7	5.7
Genera with >50 species	24	10
Families with >50 species	23	15

provide a useful comparison. SWA occupies generally lower latitudes than SEA (SWA 27°–35°S; SEA 33°–39°S). Hooker (1859) included Tasmania in his SEA; however, while Tasmania has clear affinities with mainland southeastern Australia and is connected to it during periods of low mean sea level, we exclude it here because it extends substantially further south (to 43°S), greatly increasing the environmental differences between the two regions. The areas of the two regions as defined are approximately equal (Table 1).

Species checklists for each bioregion based on vouchered specimen records held in Australian herbaria were obtained from http://avh.chah.org.au (download 2/1/2014). No attempt was made to correct for cases of probable incorrect determinations on some specimens. Only species names matching accepted names in the Australian Plant Census (APC) (CHAH 2004), and only species annotated in the APC as native for the region in question, were included. Higher-level taxonomy follows the APC. Table 1 provides core statistics for the two areas.

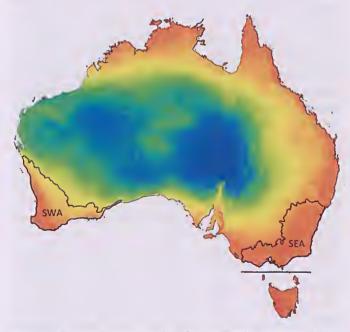


Figure 1 Mean aridity index for Australia (source: Atlas of Living Australia, red to blue indicates increasing aridity). Southwest Australia (SWA) and southeast Australia (SEA) as defined in this paper (see text) are outlined. SWA is well bounded by arid lands to the north and east; SEA is not.

Hooker's observations still stand that SWA is richer in species and poorer in genera and families than SEA; hence, its genera and families are on average more species-rich. SWA has 1.4 times more species than SEA; conversely, SEA has 1.3 times more genera and families than SWA. SWA genera on average have 10 species compared with 5 in SEA, and SWA families have on average 57 species compared with 30 in SEA.

His conclusion that most of the larger SWA genera are small or absent in SEA can no longer be supported (Table 2), although it is still the case that for most (75%) of the

Table 2 Genera with >50 species occurring in Southwest Australia (SWA) and Southeast Australia (SEA)

,	•			
Genus	SWA species	SEA species	SWA/SEA species	
Acacia	440	226	2.0	
Eucalyptus	294	230	1.3	
Leucopogon	204	32	6.4	
Stylidium	200	13	15.4	
Grevillea	195	94	2.1	
Melaleuca	174	29	6.0	
Banksia	156	14	11.1	
Caladenia	110	82	1.3	
Gastrolobium	106	0	-	
Hakea	100	28	3.6	
Hibbertia	97	46	2.1	
Verticordia	94	0	-	
Daviesia	91	15	6.1	
Drosera	91	11	8.3	
Baeckeaa	85	10	8.5	
Eremophila	81	17	4.8	
Goodenia	62	34	1.8	
Synaphea	60	0	-	
Darwinia	58	12	4.8	
Schoenus	58	23	2.5	
Petrophile	56	4	14.0	
Boronia	52	38	1.4	
Calytrix	52	3	17.3	
Hemigenia	51	2	25.5	

^a Baeckea is a phylogenetically diverse genus and is poorly resolved taxonomically; most of the taxa currently included in it, in both SWA and SEA, will be moved to other genera in future taxonomic revisions (M E Trudgen & B Rye pers. comm. 2014)

Table 3 Families occurring in Southeast Australia (SEA) and not in Southwest Australia (SWA), and vice versa.

Families found in SEA and not in SWA	Families found in SWA and not in SEA
Endemic to A	Australia
Atherospermataceae,	Anarthriaceae, Byblidaceae,
Blandfordiaceae, Doryanthaceae,	Cephalotaceae,
Eupomatiaceae,	Ecdeiocoleaceae,
Petermanniaceae	Emblingiaceae
Non-ende	emic
Alseuosmiaceae, Amaryllidaceae,	Apodanthaceae,
Anacardiaceae, Arecaceae,	Combretaceae,
Argophyllaceae, Asteliaceae,	Pedaliaceae, Surianaceae
Burmanniaceae, Cabombaceae,	
Caprifoliaceae, Ceratophyllaceae,	
Cornaceae, Corynocarpaceae,	
Cunoniaceae, Ebenaceae,	
Eriocaulaceae, Flagellariaceae,	
Gesneriaceae, Icacinaceae,	
Luzuriagaceae, Lythraceae,	
Melastomataceae, Meliaceae,	
Menispermaceae, Monimiaceae,	
Nothofagaceae, Orobanchaceae,	
Paracryphiaceae, Passifloraceae,	
Pennantiaceae, Phytolaccaceae,	
Piperaceae, Pontederiaceae,	
Putranjivaceae, Ripogonaceae,	
Salicaceae, Sapotaceae,	
Smilacaceae, Sparganiaceae,	
Symplocaceae, Thismiaceae,	
Trimeniaceae, Verbenaceae,	
Winteraceae, Zingiberaceae	

shared, large genera, SWA is proportionately richer than the 1.4x overall average for the two areas.

Hooker's conclusion that many taxa that occur in SEA but not in SWA have significant alliances outside Australia is still valid (Table 3). 90% of families (44/49) found in SEA but not SWA have significant representation outside Australia, while only 44% of the small number of families (4/9) found in SWA but not SEA have representation outside Australia.

Within the overall trend towards higher species richness in SWA, a wide range in relative richness is shown by different families (Table 4). Of families that occur in both regions, Stylidiaceae, Droseraceae, Restionaceae, Proteaceae, Goodeniaceae, Ericaceae and Myrtaceae are highly to moderately SWA-skewed (SWA:SEA species ratio 13.9:2.8), while Rubiaceae, Juncaceae, Plantaginaceae, Poaceae, Polygonaceae and Campanulaceae are moderately to slightly SEA-skewed (SEA:SWA species ratio 4.1:1.6). Other families (e.g. Santalaceae, Casuarinaceae, Solanaceae, Sapindaceae, Celastraceae) show no strong skew, being equally rich in both areas.

The observation by Hooker and others that SWA has a higher overall endemism, at both species and genus level, remains valid, although Hopper & Gioia (2004) noted

Table 4 Families shared between Southwest Australia (SWA) and Southeast Australia (SEA) and with at least 10 species in each.

Family	SWA species	SEA species	SWA:SEA	SEA:SW
Stylidiaceae	208	15	13.9	0.1
Droseraceae	92	12	7.7	0.1
Restionaceae	108	26	4.2	0.2
Proteaceae	732	215	3.4	0.3
Goodeniaceae	208	64	3.3	0.3
Ericaceae	339	114	3.0	0.3
Myrtaceae	1177	428	2.8	0.4
Malvaceae	136	50	2.7	0.4
Scrophulariaceae	95	38	2.5	0.4
Asparagaceae	104	44	2.4	0.4
Portulacaceae	32	15	2.1	0.5
Dilleniaceae	97	46	2.1	0.5
Loganiaceae	27	14	1.9	0.5
Fabaceae	1010	525	1.9	0.5
Boraginaceae	25	13	1.9	0.5
Aizoaceae	21	11	1.9	0.5
Amaranthaceae	42	22	1.9	0.5
Lamiaceae	179	94	1.9	0.5
Elaeocarpaceae	36	23	1.6	0.6
Polygalaceae	17	11	1.5	0.7
Pittosporaceae	36	24	1.5	0.7
Thymelaeaceae	46	33	1.4	0.7
Juncaginaceae	16	12	1.3	0.8
Hemerocallidaceae	34	26	1.3	0.8
Apiaceae	56	44	1.3	0.8
Rhamnaceae	96	76	1.3	0.8
Euphorbiaceae	59	47	1.3	0.8
Haloragaceae	52	43	1.2	0.8
Lentibulariaceae	14	12	1.2	0.9
Santalaceae	28	25	1.1	0.9
Casuarinaceae	28	26	1.1	0.9
Solanaceae	43	42	1.0	1.0
Sapindaceae	30	33	0.9	1.1
Celastraceae	15	17	0.9	1.1
Araliaceae	36	42	0.9	1.2
Rutaceae	127	151	0.8	1.2
Cyperaceae	176	212	0.8	1.2
Brassicaceae	40	53	0.8	1.3
Phyllanthaceae	14	19	0.7	1.4
Asteraceae	303	438	0.7	1.5
oranthaceae	13	19	0.7	1.5
Convolvulaceae	15	23	0.7	1.5
Orchidaceae	296	472	0.6	1.6
Campanulaceae	23	37	0.6	1.6
olygonaceae	11	25	0.4	2.3
oaceae	147	380	0.4	2.6
lantaginaceae	14	41	0.3	2.9
ıncaceae	14	52	0.3	3.7
lubiaceae	15	61	0.2	4.1

The columns SWA:SEA and SEA:SWA give the proportional representation in the two regions. Families in bold have high numbers of oligotrophic-soil specialists

that estimates of endemism of the SWA flora have been steadily revised downwards in recent years. Analyses of these data show that 52% of SWA species and 10% of genera are endemic; by comparison, 14% of SEA species and 1% of SEA genera are endemic to the region as defined.

The average size of species ranges (area of occupancy, distributional area) of species in SWA and SEA was not tested for this analysis. However, Hooker's observation that SWA is characterised by species with restricted distributions compared with SEA still stands. González-Orozco *et al* (2011), in a gridded, continent-wide analysis of distributional data for *Acacia*, showed that many grid cells in SWA included narrowly endemic species (i.e. species found in one grid cell but not its neighbours), but that few in SEA showed the same pattern.

The contention of Hopper *et al.* (1996) and Hopper & Gioia (2004) that SWA is unusually rich in small, monotypic and phylogenetically isolated lineages is not supported by this analysis. While these papers do not rigorously define the concept of an isolated lineage, their examples principally equate to small SWA families as candidates for phylogenetically isolated lineages. This analysis shows that five Australian-endemic families found in SWA and not SEA (Table 3) are all small and/or monotypic; however, the same can be said for the five Australian-endemic families found in SEA and not SWA.

In addition to the features noted by Hooker (1859), two further special characteristics of the SWA flora have been noted in the literature: its high morphological richness, and the high proportion of species that are oligotrophic specialists. Carlquist (1974) described a high morphological variance in SWA species of genera and families shared with SEA. In genera such as Eucalyptus, Melaleuca, Banksia, Hakea, Acacia, Daviesia, Leucopogon and Goodenia and families such as Rutaceae, Rhamnaceae and Stylidiaceae there is a consistent pattern in which 'unusual' morphologies are found in representatives and not in SEA ones. Examples include extremes in cladode morphology in Daviesia, flower and fruit size in Eucalyptus, leaf morphology in Hakea and flower colour in Goodenia. While not yet formally tested, the observational evidence is strong that in many groups the SWA flora has a wider morphological amplitude than the SEA flora.

The large number of SWA plants that have specialised adaptations for oligotrophic (particularly P- and micronutrient-limited) soils has often been noted (Pate & Dell 1984; Lambers et al. 2010). In general, these are plants that are characteristic of kwongan on sandplains; while many habitats in SWA (and indeed in SEA) are highly oligotrophic on a global scale (Lambers et al. 2010), sandplains are among the most nutrient-limited in the region. Adaptations include cluster roots, parasitism and carnivory (see Lamont 1982 for review). Plants that lack these features but are nevertheless well represented in kwongan (e.g. many Myrtaceae) are assumed to have physiological mechanisms that allow them to cope with low nutrient levels. Oligotrophy-specialists are significantly over-represented among SWA-skewed families (Table 4: four of the five most-skewed families are oligotrophy-specialists), and are almost absent from SEA-skewed families.

EXPLANATIONS OF SPECIAL CHARACTERISTICS OF THE SWA FLORA

While Hooker regretted his inability to adequately explain the special characteristics of the SWA flora, subsequent authors have provided multiple explanations, favouring either single causes or multiple interacting factors that may have been important, particularly in generating its high species richness and endemism.

Diels (1906) considered that the most important difference between the floras of SWA and SEA was an almost complete lack of two significant elements—the Malaysian and Antarctic—in the SWA flora, regarding it as almost entirely autochthonous (reprising Hooker's comment that the SWA flora is 'characteristically Australian': see also Nelson 1981). He proposed competition between these two non-autochthonous and the autochthonous element in SEA as an explanation for its lesser species richness. He provided no mechanism for this competitive limitation of overall species richness, and the concept of distinct elements in the Australian biota is now largely abandoned.

Modern authors have framed hypotheses around four key factors. Two of these, environmental instability and environmental stability, focus on historical factors affecting current richness while two, habitat diversity and oligotrophy, while acknowledging that speciation occurs over time and hence history is important, are essentially ahistorical and focus on current ecological processes as explanatory.

Environmental instability

A frequent explanation for the high species diversity in SWA (Burbidge 1960; Hopper 1979; Hopper & Maslin 1978; Cowling et al. 1996) is that fluctuating environments during glacial cycles of the Quaternary led to a recent burst of genetic divergence (Byrne et al. 2011) and speciation, especially along the margins of SWA where rainfall is transitional between the mesic and eremaean zones. A proposed mechanism is recurrent restriction of species to small, fragmented populations as arid conditions swept across the SWA's edaphically complex landscape (Nelson 1981), resulting in rapid genetic drift and/or adaptation and hence rapid speciation.

Environmental instability may or may not provide a plausible explanation for high species richness and high genetic structuring in many SWA species. Environmental stresses associated with rapidly fluctuating climate cycles in the Quaternary might be expected to result in both high extinction and high speciation rates. Higher species richness can only result if speciation exceeded extinction during these phases of environmental stress, but an emerging consensus in the literature is the opposite (Jansson & Dynesius 2002; Jansson & Davies 2008). Indeed, Dynesius & Jansson (2000) argued that rapidly fluctuating climate both increases extinction and decreases speciation (by accelerating local extinction or blending of diverging gene pools). Even if environmental instability can increase species richness, it can only explain the differences between SWA and SEA if glacial cycles were either more pronounced or more effective in SWA than SEA. While SWA is edaphically complex, SEA is topographically complex, so the same mechanism could apply there. Byrne *et al.* (2011) provided examples of phylogeographic structuring throughout the whole mesic biome in Australia, without singling out SWA as distinctive.

Environmental stability

Sniderman et al. (2013) suggested that Pleistocene stability rather than instability can explain SWA's richness. They described a hyperdiverse early Pleistocene, non-mediterranean sclerophyllous fossil flora from Victoria (SEA), and proposed that a major Pleistocene sclerophyllous extinction occurred in SEA but not SWA, perhaps because the latter was climatically more stable during this time. Other authors have invoked stable environmental conditions over longer time frames to explain the special characteristics of the SWA flora. Marchant (1973 p. 28) considered that SWA's endemism and richness became progressively established from the late Eocene and Miocene due to the 'long-standing stability of the western plateau'. Hopper (2009) elaborated this idea, proposing that much of SWA has been climatically buffered for the past 100 Ma and that a combination of a low average rate of extinction and moderate, recurrent episodes of speciation over long periods resulted in a slow build-up of richness and endemism. This is similar to the 'tropical conservatism hypothesis' (Wiens & Donoghue 2004) for high species richness in the tropics.

As an explanation for high species richness in SWA. environmental stability has the advantage that it is concordant with some broad-scale explanations of global species richness (see Mittelbach et al. 2007 for review); SWA and similar areas are anomalously rich because they have been anomalously climatically stable for long periods of time. As an explanation of SWA's higher species richness than SEA, it relies on a contrasting lack of historical climatic stability (and hence higher extinction rates or lower speciation rates) in SEA. This, however, would render the lower generic and family richness in SWA paradoxical; more stable climates should favour the persistence of families and genera as well as species. The reverse appears to have been the case in SWA, hence for environmental stability to explain SWA's high species richness, there would need to be an alternative explanation for its lower generic and family richness.

Habitat diversity and patchiness

Environmental diversity, especially when combined with habitat patchiness, is the primary driver of beta diversity, and higher beta diversity in a given region would be expected to lead to higher total species richness. Burgman (1988) observed very high levels of beta diversity in sandplain and halophyte habitats in SWA, regarded that this could not be adequately explained by soil or climate parameters, and suggested that the relative isolation of habitat patches may explain the high turnover rates. While SWA landscapes are topographically subdued, the edaphic complexity of much of SWA may provide high levels of habitat variation at local to regional scales. Allopatric speciation caused by reduced gene flow between patches may then drive species richness higher over time, associated with short-range endemism of the resulting species.

To explain higher species richness in SWA than SEA, a comparison would need to show that SWA is patchier than SEA. Parts of SWA are clearly edaphically complex, leading to patchier vegetation (see Hopper 1979 figure 4). An interesting question is whether the greater topographic complexity of SEA is as effective in driving allopatric speciation as the greater edaphic complexity of SWA.

Oligotrophy

SWA appears to have substantially more extensive areas of oligotrophic soils (sandplains, laterites) than SEA (although a rigorous comparison of soils in SWA and SEA has not been attempted). Oligotrophic soils in SWA, for reasons still unclear, support high species diversity including both high alpha (Hopkins et al. 1983) and beta (Burgman 1988) diversity. Oligotrophy specialists are dominant in kwongan, and kwongan is most extensive in parts of SWA that have the highest species richness. Similarly, a long-standing observation in SEA (Diels 1906; González-Orozco et al. 2011; Rice & Westoby 1983) is that the oligotrophic Hawkesbury Sandstone (New South Wales) is unusually species-rich and on a par with SWA; Blue Mountains National Park on Hawkesbury Sandstone has a higher species richness in a somewhat smaller area than Fitzgerald River National Park, a noted diversity hotspot, in SWA (Table 5). Rice & Westoby (1983) hypothesised that richness in the Hawkesbury system is principally determined by oligotrophy rather than climate or history.

The 'niche-dimension' hypothesis (Hutchinson 1957) provides a context for understanding high species richness on oligotrophic soils. While acknowledging the importance of time and evolutionary processes, this focuses instead on ecological conditions. It suggests that some areas or habitats are richer in species than others due to intrinsic ecological factors, such as greater niche dimensionality associated with trade-offs among species in their capacity to compete for multiple limiting resources (Harpole & Tilman 2007; Harpole and Suding 2011), including partitioning among different forms of soil P (Laliberté *et al.* 2013). Perhaps if SEA had areas of oligotrophic soils as extensive as those in SWA it would be as species rich.

A FRAMEWORK FOR UNDERSTANDING SPECIES RICHNESS IN SWA AND SEA

The explanations and hypotheses for differing species richness in SWA and SEA can be reduced to two key

Table 5 Species richness in Blue Mountains and Fitzgerald River National Parks.

	Area (km²)	Native angiosperm species
Blue Mountains National Park	2482	1456 a
Fitzgerald River National Park	3299	1402 ь

^a Source http://www.bionet.nsw.gov.au, download 1/1/14

^bSource http://naturemap.dec.wa.gov.au, download 1/1/14

framing questions: how many species can 'fit' in each region (determined by niche richness and habitat diversity), and of the species that can potentially fit, how many are actually present (determined by extinction, speciation and immigration operating over historical time frames). In any given area after a suitable length of time without perturbation, a dynamic equilibrium should be reached where as many species are present as can fit, species addition (through speciation and immigration) balances species subtraction (by extinction) and richness has reached its potential and will neither increase nor decrease over time. If SWA and SEA can potentially fit the same number of species, then SEA must be further below equilibrium than SWA and historical factors are needed to explain this. If, however, SWA can fit more species than SEA, then both may be at the same distance from equilibrium and historical factors may be unimportant.

Nine scenarios can be envisaged depending on the answers to these two questions (Table 6). For the SWA–SEA comparison at species level, four scenarios (5, 6, 8, 9) can be discounted as they fail to predict the observed SWA's higher richness. Three scenarios (1, 2, 4) predict greater richness in SWA, while two scenarios (3, 7) are ambiguous and may result in either more, the same, or less richness depending on the balance between factors.

The five plausible scenarios are: (i) Scenario 1, more species can fit in SWA, and SWA is closer to equilibrium than SEA (e.g. if SWA has more niches than SEA and a more stable climate history); (ii) Scenario 2, as many species can fit in SWA as SEA, and SWA is closer to equilibrium than SEA (e.g. if both areas have equivalent niche richness and SWA had a more stable climate history); (iii) Scenario 3, fewer species can fit in SWA, but SWA is closer to equilibrium than SEA (e.g. if SWA has fewer niches but a more stable climate history); this scenario may result in more, equal or fewer species in SWA depending on how much the positive effect of a more stable climate history offsets the negative effect of reduced niche richness); (iv) Scenario 4, more species can fit in SWA, and SWA and SEA are equally close to equilibrium (e.g. if SWA has more niches, and both areas have experienced equivalent climate histories); and (v) Scenario 7, more species can fit in SWA, but SWA is further from equilibrium than SEA (e.g. if SWA has more niches, and a less stable climate history); this scenario may result in more, equal or greater species richness in SWA depending on how much the positive effect of extra niche richness offsets the negative effect of more recent extinction or reduced speciation).

A central problem remains the need to understand exactly what differences (if any) in the environmental histories and ecological conditions of SWA and SEA are relevant to the development of its higher species richness. Both history-dependent and history-independent scenarios may be equally plausible. Thought experiments are useful here: would SEA and SWA differ in richness if: (i) both had similar current ecological conditions (e.g. equally large areas of oligotrophic soils) but retained their differences in evolutionary history; or conversely (ii) both had similar evolutionary histories but retained their differences in ecological conditions. Such thought experiments may help tease out the relative importance of these factors.

QUESTIONS, APPARENT PARADOXES, AND GAPS IN OUR UNDERSTANDING OF THE FLORA OF SWA AND ITS HISTORY

While much has been achieved since Hooker's time in documenting and understanding floristic patterns both within and between SWA and SEA, much remains to be understood; paradoxes and knowledge gaps remain. Five issues surrounding the flora of SWA that require further explanation and analysis are discussed briefly below. New tools that have become available since Hooker's time, particularly well-resolved and dateable molecular phylogenies and spatial analysis tools, may make some of these questions more tractable.

Is the higher endemism of SWA than SEA noteworthy?

Along with high species richness, the high endemism (although with steadily declining values, see above) in SWA is usually considered one of its most noteworthy aspects, particularly when compared with much lower values in other parts of Australia (Crisp et al. 1999). However, SWA is an ecological island with a relatively natural boundary, while SEA is not. Islands are noted for their high endemism, generated by reduced opportunities for recent immigration (and hence shared taxa) and increased opportunities for within-island radiations (MacArthur & Wilson 1967). SEA, by contrast, is contiguous with regions to the north, east and south that share its mesic environment. Hence, many plant species extend beyond the region as defined, and its endemism value is predictably low. However, the higher species richness of SWA compared with SEA is not predictable from these differences, and in many ways is more remarkable than its higher endemism.

Table 6 A simplified framework for comparing species richness in two different areas. Values in cells give expected comparative richness in Southwest Australia (SWA) compared with Southeast Australia (SEA) under nine different scenarios (numbered in parenthesis).

	How many species can fit in SWA compared with SEA?						
		1	More	The sa	me number	1	Fewer
How close is SWA	Closer	(1)	Richer	(2)	Richer	(3)	?
to equilibrium	The same	(4)	Richer	(5)	Equal	(6)	Fewer
compared with SEA?	Further	(7)	?	(8)	Fewer	(9)	Fewer

Why is SWA depauperate at genus and family level?

While the relatively depauperate nature of the flora of SWA at genus and family level has been known since Hooker's time (and confirmed in this analysis), it has received much less attention than the area's higher species richness and endemism. As with species richness, few comparative studies have been attempted to explain why SEA would be richer in genera and families but poorer in species than SWA. Extinction has been invoked to explain the absence from SWA of plants from the Tertiary rainforests (Hopper 1979) and of a suite of mesicforest vertebrates (gliding possums, lyrebirds, logrunners) that presumably lived in them (Archer 1996). Similarly, extinctions have played a major role in shaping the flora of SEA (Crisp & Cook 2011). However, extinction alone cannot adequately explain the opposing trend in species cf. family and genus richness, without a further explanation as to why it would affect these different taxonomic levels differently.

Again, as with the difference in species richness, both historical and ahistorical explanations are plausible. An early phase in SWA where extinction exceeded speciation may have led to reduced richness at all taxonomic levels, followed by a phase where speciation exceeded extinction in the remaining genera and families (leading to a near-equilibrium state at species level but retaining a below-equilibrium state at higher taxonomic levels). Alternatively, recent extinctions in SWA of taxonomic groups that are rich in genera and families but relatively poor in species (or persistence or recolonisation into SEA of such groups) could explain the skew. Rainforest taxa, which are relatively well-represented in SEA but virtually absent from SWA, may be one such group. The scenarios may also be inverted: major extinctions in SEA (Sniderman et al. 2013) may have preferentially involved species-rich families and genera. Such scenarios, of course, merely shift the explanatory burden for the observed skew from areas (SWA cf. SEA) to taxonomic or ecological groups (rainforest cf. non-rainforest taxa). An ahistorical explanation for such skews can also be envisaged, for example if relatively few genera and families are capable of extensive radiations in SWA's oligotrophic soils.

Are observed patterns of species richness within SWA historically meaningful?

Many authors have mapped species richness within SWA and attempted to identify nodes of higher-than-average or lower-than-average richness within the area, both for individual families or genera (Speck 1958; Hopper & Maslin 1978; Lamont et al. 1982) and for the vascular flora as a whole (Hopkins et al. 1983; Hopper & Gioia 2004). Repeated patterns are found, with nodes of species richness in the northern and/or south-coastal sandplains, and the wet forests of the far southwest generally having low diversity. Across the entire flora, however, other patterns also exist: Acacia is richest in the wheatbelt (Hopper & Maslin 1978; Hnatiuk & Maslin 1980), Eucalyptus has a node of species richness in the Great Western Woodlands, while Hopper & Gioia (2004) identified a third node of richness on the Swan Coastal Plain.

As with overall richness, either or both historical and ahistorical factors may be explanatory for these patterns.

Hopper (1979) used these patterns in support of a Quaternary speciation burst in the area of intermediate rainfall designated the Transitional Rainfall Zone, while Hopper & Gioia (2004) used them to infer historical climatic stability (hence low extinction rates) in the near-coastal parts of the Transitional Rainfall Zone. However, these nodes of high species richness are also co-extensive with the largest and most contiguous areas of oligotrophic sandplains, and hence kwongan vegetation, in SWA, and the oligotrophy itself might drive the species richness.

While the patterns are undeniably real, random speciation occurring across an area would be expected to generate some pattern, including nodes of higher-than-average richness, through chance alone. No analysis has yet attempted to reject a null hypothesis of random chance for these patterns. Further, some aspects of the observed pattern (such as the low species richness in the far southwest) may be significantly different from a null model, while other parts of the pattern (such as the high-richness nodes in the Mt Lesueur, Stirlings–Fitzgerald River areas or Swan Coastal Plain) may not.

Few equivalent analyses identifying nodes of species richness are available for SEA. Hnatiuk & Maslin (1980) and González-Orozco *et al.* (2011) produced richness maps for *Acacia* for the whole of Australia, which clearly demonstrate the relatively richer flora of SWA compared with SEA, and showed a number of SEA richness nodes including the Blue Mountains. It is likely that similarly congruent patterns will be found there, perhaps allowing more powerful tests and more general inferences than those based on SWA alone.

Why have some taxonomic groups been insensitive to SWA's special circumstances?

Different plant groups appear to have responded differently to the different conditions, historical or ecological or both, in SWA and SEA (Table 4). Some of these differences may be due to the greater connectivity of SEA with other non-arid regions (northern New South Wales, Tasmania during sea-level minima), which would be expected to have provided abundant opportunities for recolonisation after unfavourable conditions and extinctions; such opportunities were largely unavailable or restricted for SWA. However, this is unlikely to be the sole cause of current differences. In particular, the question remains open as to why some species-rich families, such as Poaceae and Asteraceae, have not been influenced by whatever drivers of richness have operated in SWA.

Why are there very few species restricted to single (or a few adjacent) granite inselbergs in SWA?

Much of SWA is underlain by a single, geologically stable, highly eroded, Archaean, predominantly granitic crustal block, the Yilgarn Craton. The craton granites are exposed in a scatter of isolated, exposed inselbergs over much of SWA, the individual inselbergs often separated by extensive areas of alluvium, sandplain or laterite. If SWA is an ecological island, the inselbergs form an archipelago of even smaller ecological islands within the region; they and their skirts of light-textured, relatively rich and runoff-watered soils are usually well-separated by flatter, drier, heavier-textured and/or more oligotrophic soils. Many granite-specialist plants (e.g.

Eucalyptus caesia, Kunzea haxteri, various species in vernal pools on their summits) and animals occur on or around them, and are often restricted to them.

If speciation in SWA has been driven by either recent or older phases of allopatric speciation caused by climate change, or through genetic isolation in patchy habitats, then the inselbergs, especially the more isolated ones, should be ideal candidates for allopatric species radiations. It may be expected that a suite of species would be found that are very narrowly endemic, restricted to single inselbergs or closely adjacent complexes of inselbergs. On current evidence, this is not the case. Hopper et al. (1997) analysed records of orchids from an exhaustive survey of granite rocks throughout the Yilgarn Craton, and identified only two potential taxa restricted to single rocks out of 141 taxa recorded on inselbergs; this can be regarded as a background level of very narrow-range endemism in the SWA context. In some cases, inselberg specialists show genetic signals of isolation and drift [e.g. Eucalyptus caesia (Byrne & Hopper 2008); Kunzea haxteri (Tapper et al. 2014)], however, this is not usually at a level that allows taxonomic recognition. Tapper et al. (2014) estimated the deepest observed genetic divergence between populations of K. haxteri to the Pliocene, but most populations appear to show Pleistocene-age divergences; in all cases, divergences are at infra-species, population levels and have not (yet?) led to speciation.

In contrast to the situation on the granite inselbergs, Gibson *et al.* (2010) listed 10 taxa that are believed to be restricted to single banded iron formation (BIF) ranges on the edge of the Yilgarn Craton (immediately adjacent to SWA as defined here); further species are known from other BIF ranges, with more to be described in the near future. Greenstone ranges (e.g. Ravensthorpe Range) are even richer in single-range species (Markey *et al.* 2012). In this context, the apparent low prevalence of single-inselberg taxa in SWA appears to be paradoxical under current models for extensive allopatry driving speciation.

PROSPECTS FOR FURTHER WORK, AND CONCLUSIONS

Since Hooker first formalised the observation that SWA has special characteristics, regretted his inability to explain them, and proposed that understanding SWA may provide insights into general problems of evolution, many authors have sought explanations, mostly historical, for the two most striking characteristics of the SWA flora: its high species richness and endemism. Other characteristics, including its relative paucity of genera and families, have received less attention. Furthermore, most studies that have addressed these questions by comparison with other areas have used comparisons outside Australia, ignoring the area with which SWA has its closest physical, historical and floristic connections, SEA. Other studies have sought to explain SWA's special characteristics without explicit reference to outside comparisons at all, drawing conclusions based only on inferred historical processes within SWA that may or may not themselves be special.

Hooker (1859 p. xxvii) faced a similar situation at the time he was writing, pertaining to the flora of the whole

of Australia, and his comments are important in this context: 'So numerous indeed are the peculiarities of this Flora, that it has been considered as differing fundamentally, or in almost all its attributes, from those of other lands; and speculations have been entertained that its origin is either referable to another period of the world's history from that in which the existing plants of other continents have been produced, or to a separate creative effort from that which contemporaneously peopled the rest of the globe with its existing vegetation; whilst others again have supposed that the climate or some other attribute of Australia has exerted an influence on its vegetation, differing both in kind and degree from that of other climates.'

Diels (1906 p. 39) likewise felt the need to balance analyses of the differences between the regions with considerations of similarity: 'The high degree of endemism which characterizes south-western Australia has been known since Robert Brown's time, but it has always been over-rated. When, for example, Hooker (loc. cit. p. 28) states that the difference between south-eastern and south-western Australia is greater than that between Australia and the rest of the earth, he is going too far. His conclusions are based on incorrect deductions from inadequate data. A close investigation of the difference between the two sides of the continent shows that the families characteristic of the west show little difference from those of the east.'

Hopper (2009) pointed out that biogeographic and evolutionary hypotheses are only useful if they are testable, and hence able to move from narrative to analytical frameworks (Ball 1976). We add to this a further requirement, that tests should include a formal null hypothesis. In the case of SWA, one null hypothesis is 'that SWA is not special compared with other comparable regions'. The analyses with which we commenced this paper shows that this hypothesis can be rejected: some of the special characteristics raised by Hooker (1859) and discussed vigorously ever since, remain. A second null hypothesis 'that the differences in species richness between SWA and SEA are not due to differences in history', however, cannot yet be rejected and remains possible. Falsification of this null hypothesis is important, since determining exactly what needs to be explained is a necessary precursor to any explanation.

ACKNOWLEDGEMENTS

We thank David Coates, Stephen Hopper, Neil Gibson, Colin Yates and an anonymous reviewer for constructive comments and discussions on the manuscript.

REFERENCES

ARCHER M 1996. Refugial vertebrates from the Miocene rainforests of Western Australia: where are they? In: Hopper S D, Chappill J A, Harvey M S & George A S (eds) Gondwanan heritage: past, present and future of the Western Australian biota, pp. 100–103. Surrey Beatty & Sons, Chipping Norton.

Balli R 1976. Nature and formulation of biogeographical hypotheses. *Systematic Zoology* **24**, 407–430.

Beard J S 1990. Plant life of Western Australia. Kangaroo Press, Sydney.

Brown R 1810. Prodromus Florae Novae Hollandiae et Insulae Van Diemen. Richard Taylor & Son, London.

- Brown R 1814. Appendix III: General remarks, geographical and systematical, on the botany of Terra Australis. *Iu*: Flinders M A Voyage to Terra Australis, pp. 533–612. G & W Nicol, London.
- Burbidge N T 1960. The phytogeography of the Australian region. *Australian Journal of Botany* 8, 75–209.
- Burgman M A 1988. Spatial analysis of vegetation patterns in southern Western Australia: implications for reserve design. Australian Journal of Ecology 13, 415–429.
- Byrne M & Hopper S D 2008. Granite outcrops as ancient islands in old Iandscapes: evidence from the phylogeography and population genetics of *Eucalyptus caesia* (Myrtaceae) in Western Australia. *Biological Journal of the Linneau Society* 93, 177–188.
- Byrne M, Steane D A, Joseph L, Yeates D K, Jordan G J, Crayn D, Aplin K, Cantrill D J, Cook L G, Crisp M D, Keogii J S, Melville J, Moritz C, Porch N, Sniderman J M K, Sunnucks P & Weston P H 2011. Decline of a biome: evolution, contraction, fragmentation, extinction and invasion of the Australian mesic zone biota. *Journal of Biogeography* 38, 1635–1656.
- CARLQUIST S 1974. Island biology. Columbia University Press, New York.
- CHAH (Council of Heads of Australasian Herbaria) 2004. Australian plant census.Council of Heads of Australasian Herbaria http://www.chah.gov.au/apc/index.html (accessed 2/1/2014).
- COWLING R M & LAMONT B B 1998. On the nature of Gondwanan species flocks: diversity of Proteaceae in Mediterranean south-western Australia and South Africa. *Australian Journal of Botany* 46, 335–355.
- COWLING R M, RUNDEL P W, LAMONT B B, ARROYO M K & ARIANOUTSOU M 1996. Plant diversity in Mediterranean-climate regions. *Trends in Ecology and Evolution* 11, 362–366.
- CRISP M D & COOK L G 2011. Cenozoic extinctions account for the low diversity of extant gymnosperms compared with angiosperms. New Phytologist 192, 997–1009.
- Crisp M D, Laffan S, Linder H P & Monro A 2002. Endemism in the Australian flora. *Journal of Biogeography* 28, 183–198.
- Crisp M D, West J G & Linder H P 1999. Biogeography of the terrestrial flora. (Flora of Australia Vol. 1) 2nd edition. Australian Biological Resources Study, Canberra.
- DEWHA (DEPARTMENT OF THE ENVIRONMENT, WATER, HERITAGE AND THE ARTS) 2008. Interim Biogeographic Regionalisation for Australia (IBRA), Version 6.1. http://www.environment.gov.au/parks/nrs/science/bioregion-framework/ibra/index.html (accessed 1/2/2014).
- Diels L 1906. Die Pflanzenwelt von West-Australien südlich des Wendekreises (The plant life of Western Australia south of the tropic) translated by Grieve B J, Lamont B B & Hellmuth E O. In: Gibson N (ed.) Translation of Diels 1906 Plant life in Western Australia, pp. 1–373. Conservation Science Western Australia Journal 6(2).
- Dynesius M & Jansson R 2000. Evolutionary consequences of changes in species geographical distributions driven by Milankovitch climate oscillations. *Proceedings of the National Academy of Sciences* 97, 9115–9120.
- Fox M D 1996. Australian Mediterranean vegetation: intra- and intercontinental comparisons. In: Arroyo M T K, Zedler P H & Fox M D (eds) Ecology and biogeography of Mediterranean ecosystems in Chile, California, and Australia, pp. 137–159. Springer, New York
- GIBSON N, YATES C J & DILLON R 2010. Plant communities of the ironstone ranges of South Western Australia: hotspots for plant diversity and mineral deposits. *Biodiversity and Conservation* 19, 3951–3962.
- GONZÁLEZ-OROZCO C E, LAFFAN S W & MILLER J T 2011. Spatial distribution of species richness and endemism of the genus *Acacia* in Australia. *Australian Journal of Botany* 59, 601–609.
- HARPOLE W S & SUDING K N 2011. A test of the niche dimension

- hypothesis in an arid annual grassland. Occologia 166, 197-205.
- HARPOLE W S & TILMAN D 2007. Grassland species loss resulting from reduced niche dimension. *Nature* 446, 791–793.
- HILLEBRAND H 2004. On the generality of the latitudinal diversity gradient. The American Naturalist 163, 192–211.
- HNATIUK R J & MASLIN B R 1980. Phytogeography of Acacia in Australia in relation to climate and species-richness. Australian Journal of Botany 36, 361–383.
- HOOKER J D 1859. On the flora of Australia, its origins, affinities and distribution: being an introductory essay to the Flora of Tasmania. Lovell Reeve, London.
- HOPKINS A J M, KEIGHERY G J & MARCHANT N G 1983. Species-rich uplands of south-western Australia. *Proceedings of the Ecological Society of Australia* 12, 15–26.
- HOPPER S D 1979. Biogeographical aspects of speciation in the Southwest Australian Flora. *Annual Review of Ecology and Systematics* **10**, 399–422.
- HOPPER S D 1994. Plant taxonomy and genetic resources: foundations for conservation. *In:* Moritz C & Kikkawa J (eds) *Conservation biology in Australia and Oceania*, pp. 269–285. Surrey Beattey & Sons, Sydney.
- HOPPER S D 2009. OCBIL theory: towards an integrated understanding of the evolution, ecology and conservation of biodiversity on old, climatically buffered, infertile landscapes. *Plant and Soil* 322, 49–86.
- HOPPER S D, BROWN A P & MARCHANT N G 1997. Plants of Western Australian granite outcrops. *In:* Withers P C & Hopper S D (eds) *Granite outcrops symposium*, pp. 141–158. Journal of the Royal Society of Western Australia 80.
- HOPPER S D & GIOIA P 2004. The Southwest Australian Floristic Region: evolution and conservation in a global hot spot of biodiversity. Annual Review of Ecology, Evolution and Systematics 35, 623–650.
- HOPPER S D, HARVEY M S, CHAPPILL J A, MAIN A R & MAIN B Y 1996. The Western Australian biota as Gondwanan Heritage—a review. In: Hopper S D, Chappill J A, Harvey M S & George A S (eds) Gondwanan heritage: past, present and future of the Western Australian biota, pp I—46. Surrey Beatty & Sons, Chipping Norton.
- HOPPER S D & LAMBERS H 2009. Darwin as a plant scientist: a Southern Hemisphere perspective. *Trends in Plant Science* **14**, 421–435.
- HOPPER S D & MASLIN B R 1978. Phytogeography of Acacia in Western Australia. Australian Journal of Botany 26, 63–78.
- Hutchinson G E 1957. Concluding remarks. In: Warren K B (ed.) Population studies: animal ecology and demography, pp. 415–427. Cold Spring Harbor Symposia on Quantitative Biology 22.
- JANSSON R & DAVIES T J 2008. Global variation in diversification rates of flowering plants: energy vs. climate change. *Ecology Letters* 11, 173–183.
- JANSSON R & DYNESIUS M 2002. The fate of clades in a world of recurrent climatic change: Milankovitch oscillations and evolution. Annual Review of Ecology and Systematics 33, 741– 777.
- Laliberté E, Grace J B, Huston M A, Lambers H, Teste F P, Turner B L & Wardle D A 2013. How does pedogenesis drive plant diversity? *Trends in Ecology and Evolution* 28, 331–340.
- LAMBERS H, BRUNDRETT M C, RAVEN J A & HOPPER S D 2010. Plant mineral nutrition in ancient landscapes: high plant species diversity on infertile soils is linked to functional diversity for nutritional strategies. *Plant Soil* 334, 11–31.
- Lamont B 1982. Mechanisms for enhancing nutrient uptake in plants, with particular reference to mediterranean South Africa and Western Australia. *The Botanical Review* 48, 597–689.
- Lamont B B, Hopkins A J M & Hnatiuk R J 1982. The flora—composition, diversity and origins. *In*: Pate J S & Beard J S

- (eds) Kwongan, plant life of the sandplain, pp. 27–50. University of Western Australia Press, Nedlands.
- Lehmann J G C 1844-1848. Plantae Preissianae, sive enumeration plantarum quas in Australasia occidentali et meridionalioccidentali Annis 1838-1841 collegit Ludovicus Preiss. Sumptibus Meissneri, Hamburg.
- LINDLEY J 1839. A sketch of the vegetation of the Swan River Colony. James Ridgeway, London.
- MACARTHUR R H & WILSON E O 1967. The theory of island biogeography. Princeton University Press, New Jersey.
- MANNING J & GOLDBLATT P 2012. Plants of the Greater Cape Floristic Region 1: the Core Cape flora. Strelitzia 29, 1–853.
- MARCHANT N G 1973. Species diversity in the southwestern flora. Journal of the Royal Society of Western Australia 56, 23–30.
- MARKEY A, KERN S & GIBSON N 2012. Floristic communities of the Ravensthorpe Range, Western Australia. Conservation Science Western Australia Journal 8, 187–239.
- MITTELBACH G G, SCHEMSKE D W, CORNELL H V, ALLEN A P, BROWN J M, BUSH M B, HARRISON S P, HURLBERT A H, KNOWLTON N, LESSIOS H A, McCain C M, McCune A R, McDade L A, McPeek M A, Near T J, Price T D, Ricklefs R E, Roy K, Sax D F, Schluter D, Sobel J M & Turelli M. 2007. Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. *Ecology Letters* 10, 315–331.
- Myers N, Mittermeier R A, Mittermeier C G, De Fonseca G A B & Kent J 2000. Biodiversity hotspots for conservation priorities. *Nature* 403, 853–858.
- Nelson E C 1981. Phytogeography of southern Australia. *In*: Keast A (ed.) *Ecological biogeography of Australia*, pp. 733–760. Dr W Junk, The Hague.
- PATE J S & DELL B 1984. Economy of mineral nutrients in sandplain species. *In*: Pate J S & Beard J S (eds) *Kwongan—plant life of the sandplain*, pp. 227–252. University of Western Australia Press, Nedlands.

- RICE B & WESTOBY M 1983. Species richness in vascular vegetation of the West Head, New South Wales. Australian Journal of Ecology 8, 163–168.
- SAUQUET H, WESTON P H, ANDERSON C L, BARKER N P, CANTRILL D J, MAST A R & SAVOLAINEN V 2009. Contrasted patterns of hyperdiversification in Mediterranean hotspots. *Proceedings of the National Academy of Sciences* 106, 221–225.
- SNIDERMAN J M K, JORDAN G K & COWLING R M 2013. Fossil evidence for a hyperdiverse sclerophyll flora under a non-Mediterranean-type climate. *Proceedings of the National Academy of Sciences* 110, 3423–3428.
- SPECK N H 1958. The vegetation of the Darling-Irwin botanical districts and an investigation of the distribution patterns of the family Proteaceae in South Western Australia. PhD thesis, University of Western Australia, Perth (unpubl.).
- STEBBINS G L & MAJOR J 1965. Endemism and speciation in the Californian flora. *Ecological Monographs* 35, 2–35.
- TAKHTAJAN A 1986. Floristic regions of the world (transl. T J Crovello & A Cronquist). University of California Press, Berkeley.
- Tapper S-L, Byrne M, Yates C J, Keppel G, Hopper S D, Van Niel K, Schut A G T, Mucina L & Wardell-Johnson G W 2014. Isolated with persistence or dynamically connected? Genetic patterns in a common granite outcrop endemic *Diversity and Distributions* DOI: 10.1111/ddi.12185.
- VALLANCE T G, MOORE D T & GROVES E W 2001. Nature's Investigator: the diary of Robert Brown in Australia, 1801-1805. Australian Biological Resources Study, Canberra
- WIENS J J & DONOGHUE M J 2004. Historical biogeography, ecology and species richness. *Trends in Ecology and Evolution* 19, 639–644.

Received 27 January 2014; accepted 1 April 2014



Phytophthora cinnamomi in Western Australia

P A O'BRIEN* & G E ST J HARDY

Centre for Phytophthora Science & Management, School of Veterinary & Life Sciences, Murdoch University, Murdoch, WA 6150, Australia.

Phytophthora cinnamomi the agent of eucalypt dieback disease in Western Australia is a serious pathogen of many plant species around the world. The pathogen has a very wide host range. In Western Australia many species of native plants are susceptible, and a large number because they are of limited distribution are threatened with extinction. This paper reviews the mechanisms by which P. cinnamomi causes disease, together with the factors that contribute to the spread and survival of the pathogen allowing it cause new disease epidemics when the right conditions prevail. It also looks at possibilities for control of the pathogen by management, chemical application and biological control.

KEYWORDS: diagnostics, dieback, hemibiotroph, phosphite, Phytophthora.

INTRODUCTION

The genus Phytophthora can justifiably lay claim to containing some of the most devastating plant pathogenic species ever seen. Nearly 200 years after our first encounter with Phytophthora as the causative agent of the Irish Potato Famine, we have identified over 121 species in this genus (Scott et al. 2013) although it has been estimated that there may be as many as 500 species (Brasier 2008). These are pathogens on a very wide range of horticultural, ornamental and silvicultural species and cause major problems wherever these crops are grown. More recently we have begun to appreciate their devastating impact on native ecosystems where they infect and kill a very wide range of native species. One of the most devastating species in an Australian context is Phytophthora cinnamomi, the cinnamon fungus, so named as it was first identified as a pathogen of cinnamon in Sumatra by Rands (Cahill et al. 2008).

Although deaths of jarrah (Eucalyptus marginata) trees due to a dieback disease had been recorded in Western Australia since the 1920s, it was not until the 1960s that infection by P. cinnamomi was linked to these deaths (Podger et al. 1965). Subsequently P. cinnamomi was found to be the cause of dieback disease in forests of East Gippsland, the Brisbane Ranges, Wilsons Promontory and the Grampians in Victoria (Weste 1994). Since then 2284 of the 5710 described native plant species in the southwest corner of Western Australia have been shown to be susceptible to P. cinnamomi of which 800 are regarded as being highly susceptible (Shearer et al. 2004a). Since many of these are of localised distribution they are easily brought to the brink of extinction.

In Australia, *P. cinnamomi* is regarded as a threat to the existence of 10% of plant species currently listed as threatened under the Environment Protection and Biodiversity Conservation Act.

Despite being widely distributed within Australia, *P. cinnamomi* is considered to have been a relatively recent introduction to Australia (Cahill *et al.* 2008). This is based

on the lack of resistance in native Australian species and lack of genetic diversity in the Australian *P. cinnamomi* population (Old *et al.* 1988; Dobrowolski *et al.* 2003). Plant pathogens often cause little damage to their hosts at their centre of origin having developed a natural balance through co-evolution with their hosts (Brasier 2008; Hansen 2008) However, problems arise when pathogens are introduced to other regions of the world where the checks and balances that normally keep the pathogen at bay are absent. Pathogens also tend to have a greater genetic diversity at their centre of origin (Fry *et al.* 1992). Analysis of a worldwide population of *P. cinnamomi* showed that the greatest degree of genetic diversity occurs in Papua New Guinea (Old *et al.* 1988; Dobrowolski *et al.* 2003).

TAXONOMY AND PHYLOGENY OF PHYTOPHTHORA

The Phylum Oomycota to which the genus Phytophthora belongs, display typical fungal characteristics such as mycelial growth and on this basis has traditionally been included in the Kingdom Mycota. This has complicated the development of disease management strategies, as oomycetes do not always respond well to strategies that are effective against fungal diseases. On the basis of biochemical, physiological and genome sequencing data the oomycetes are now grouped with the biflagellate heterokont (unequal flagellae) organisms in an assembly called the Stramenopiles (Hardham 2005; Tyler et al. 2006; Beakes et al. 2012). Stramenopiles together with the alveolate ciliates and the dinoflagellates constitute the Chromoalveolate Superkingdom (Beakes et al. 2012). Comparative genome analysis suggests a photosynthetic origin for the oomycetes. Plant pathogenic oomycetes such as Phytophthora are closely related to another group of Chromalveolate obligate parasites, the Apicomplexans that includes pathogenic species to humans such as the malarial parasite Plasmodium falciparum, and the pathogens Cryptosporidium parvum and Toxoplasma gondii the causes of cryptosporidiosis and toxoplasmosis, respectively, both of which are severe intestinal tract diseases of humans.

^{*} Corresponding author M P.OBrien@murdoch.edu.au

The most recent phylogenetic analysis of the genus *Phytophthora* encompasses 121 species divided into 10 well-supported clades (Scott *et al.* 2013). However, with the increased application of DNA sequencing technology to taxonomic studies, many species are being re-classified whilst new ones are being discovered all the time (Burgess *et al.* 2009; Scott *et al.* 2009). In the last decade the number of *Phytophthora* species has doubled (Brasier 2008).

GROWTH AND LIFE CYCLE OF P. CINNAMOMI

Phytophthora cinnamomi is considered to be a necrotrophic pathogen (Cahill et al. 2008). It grows vegetatively as a mycelium with hyphae that have few or no septa. It reproduces asexually by differentiation of the vegetative hyphae into sporangia which eventually burst to release numerous motile zoospores (Figure 1) (Hardham 2005). These are chemotactically attracted to plant roots and swim towards them and encyst on the surface. The encysted zoospores germinate by producing a germ tube that penetrates the host tissues to begin the infective

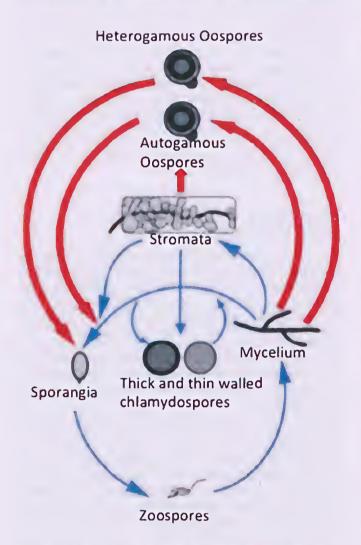


Figure 1 Life cycle of *P. cinnamonii* as modified by Crone. The life cycle is expanded from previous versions (Hardham 2005) to allow for the production of selfed oospores, stromata and thick walled chlamydospores.

cycle. Zoospores can be carried some considerable distances by moving water and are considered largely responsible for the downslope spread of the disease in favourable warm and moist environments (Cahill *et al.* 2008).

The ability to reproduce asexually is probably a major factor in the success of *Phytophthora* spp. as pathogens (Shea & Broadbent 1983). In some species the sporangia can detach from the mycelium and act as a dispersal propagule for the pathogen; e.g. in *P. iufestaus* detached sporangia can be carried distances of several kilometres (Gregory 1983). Sporangia can also be spread by water flow or splash. Soil microorganisms stimulate sporangial production in *P. ciunanuoni* (Shea & Broadbent 1983). Variations in the number of sporangial-stimulating organisms, or in the numbers of microorganisms antagonistic to them probably contribute to variation in disease development at different sites.

P. cinuamouii also produces asexual chlamydospores within the soil or planttissues. The wall of the chlamydospore is normally 0.5 µm thick, although under certain circumstances chlamydospores with especially thick walls (5 µm) are produced (Table 1) (McCarren et al. 2005). We have observed thick-walled chlamydospores in tissues of two herbaceous perennial species, Chamaescilla corymbosa and Stylidium diuroides and one annual Trachymena pilosa infected by P. cinnamonii in naturally infested sites in the jarrah forest in Western Australia (Crone et al. 2012). They have also been observed in the roots of Banksia graudis (Jung et al. 2013). P. cinnamonii can survive for several years in soil in the absence of a host and in the past it was generally considered that chlamydospores are the main survival structures. However, definitive evidence on this is lacking, and recent research findings indicate other survival strategies could account for the pathogen's longterm survival in infested areas.

Another type of asexual structure that occurs in *P. ciunauuoni* infected tissue and has only recently been observed for the first time is the stromata (Crone *et al.* 2012; Jung *et al.* 2013). Stromata are dense intermingled hyphal aggregations that can survive adverse conditions. We have observed these to germinate *iu planta* with multiple germ tubes that are capable of producing chlamydospores and selfed oospores (Crone *et al.* 2012). We speculate that stromata also serve to obtain nutrients from the host plant, which in turn allows the pathogen to produce numerous chlamydospores and selfed oospores when conditions for the pathogen become adverse. Stromata have also been observed in nine woody species found in the jarrah forest (Jung *et al.* 2013).

Sexual reproduction in *Phytophthora* occurs by fertilisation of the oogonium with a nucleus from the antheridium (Erwin & Ribeiro 1996). With heterothallic species the antheridium and oogonium are on different mycelia with different mating types (A1 and A2), whereas with homothallic species they are on the same mycelium (selfing). Although *P. cinuamoui* is considered to be heterothallic there is no genetic evidence for crossing between different mating types in natural populations despite the presence of both mating types at the same location (Dobrowolski *et al.* 2003). However, there have been several reports of the production of oospores from single isolates (selfing) of *P. cinuamomi*

Table 1 Reproductive structures observed in different asymptomatic host species infected with *Phytophthora cinnamomi*.

Host species		Reproductive structures observed						Reference
(Oospores	Chlamydospores*	Stromata	Thick-walled sclerenchyma cells	Thin- walled cells	Papillae and unbranched lignitubers	Branched lignitubers	
Encalyptus marginata	1	a	√	√	1	1	√	Jung et al. 2013
Banksia grandis	\checkmark	a	\checkmark	√	\checkmark	\checkmark	\checkmark	Jung et al. 2013
Xanthorrhoea preissii	\checkmark	a	\checkmark	√	\checkmark	\checkmark	\checkmark	Jung et al. 2013
Persoonia longifolia	\checkmark	_	\checkmark	√	\checkmark	\checkmark	\checkmark	Jung et al. 2013
Corymbia calophylla	\checkmark	_	\checkmark	_	\checkmark	√	√	Jung et al. 2013
Encalyptus megacarpa	√	_	\checkmark	_	\checkmark	√	√	Jung et al. 2013
Encalyptus jaksonii	\checkmark	a	\checkmark	_	\checkmark	√	\checkmark	Jung et al. 2013
Acacia blakeley	\checkmark	a	\checkmark	_	\checkmark	√	\checkmark	Jung et al. 2013
Banksia hookeriana	\checkmark	_	_	_	\checkmark	√	\checkmark	Jung et al. 2013
Banksia attennata	\checkmark	a	\checkmark	√	$\sqrt{}$	\checkmark	\checkmark	Jung et al. 2013
Banksia chamaephyton	t -	_	\checkmark	_	\checkmark	\checkmark	\checkmark	Jung et al. 2013
Banksia occidentalis	\checkmark	_	_	_	\checkmark	\checkmark	_	Jung et al. 2013
Eremaea panciflora	\checkmark	_	_	_	\checkmark	\checkmark	\checkmark	Jung et al. 2013
Hakea eneabba	$\sqrt{}$	_	\checkmark	-	\checkmark	\checkmark	\checkmark	Jung et al. 2013
Kımzea acuminata	_	_	\checkmark	√	\checkmark	\checkmark	√	Jung et al. 2013
Lambertia multiflora	\checkmark	a	\checkmark	√	\checkmark	\checkmark	\checkmark	Jung et al. 2013
Chamaesilla corymbosi	a √	b	\checkmark	_	_	-	_	Crone et al. 2012
Trachymena pilosa	V	b	· √	_	_	_	_	Crone et al. 2012
Stylidium diuroides	\checkmark	b	V	_	_	_	_	Crone et al. 2012

^{*}a, thick-walled chlamydospores; b, thin-walled chlamydospores

(Mircetich & Zentmeyer 1966; Jayasekera et al. 2007), while Crone et al. (2012) reported prolific oospore production in tissues of the herbaceous perennial species Chamaecsilla corymbosa and Stylidium diuroides, as well as in the annual Trachymena pilosa. Jung et al. (2013) also observed selfing to occur in a number of native Australian woody species and Mbaka et al. (2010) reported selfing in macadamia plants in Kenya. The selfed oospores observed in many of the native species in Western Australia had thicker walls than those that formed in mating tests between A1 and A2 types in agar culture and this may contribute to the survival of the pathogen over the hot dry Mediterranean summers in Western Australia.

The formation of selfed oospores appears to be stimulated by the presence of antagonistic organisms or by root exudates of certain species. On agar plates the presence of Trichoderma species stimulates selfing in P. cinnamomi (Brasier 1975). This effect appears to be associated with inhibition of hyphal growth by Trichoderma. Selfing can also be stimulated by root exudates from plants. Oleic acid present in root extracts of avocado initiated oospores in the A2 mating types of P. cinnamomi, P. cryptogea and P. capsici, but was not effective on the A1 type of P. cinnamomi (Zentmyer 1979). Exudates from Acacia pulchella stimulated oospore formation by P. cinnamomi in infected Lupinus angustifolius roots incubated for seven days under potted Acacia pulchella plants, or in soils collected from under and near varieties of A. pulchella in the jarrah forest (Jayasekera et al. 2007).

INTERACTION OF P. CINNAMOMI WITH THE HOST PLANT

The interaction with the host begins by infection of the root tips by zoospores that are chemotactically attracted to the roots. Infections can also be initiated by growth of hyphae between the roots of different species as the roots are often in contact (Shearer & Tippett 1989). Lesions may extend up to the collar, and may girdle the tree. Water transport is inhibited in susceptible but not in resistant species even though only a small proportion of the root system may be infected (Weste 1994). Once the pathogen has entered the plant tissue it rapidly colonises the wood (Davison et al. 1994). Colonisation of woody tissue was more extensive in pine compared to E. marginata (jarrah) which is relatively resistant to infection. Shearer & Tippett (1989) speculated that bark thickness may be a component of resistance although some banksias and eucalypts with thick bark are still quite susceptible (G E St J Hardy unpubl. data).

The extent of colonisation is markedly affected by environmental conditions such as temperature, moisture and the physiological status of the host. The optimal temperatures for growth in secondary phloem of *Banksia grandis* is 25–30 °C (Shearer & Tippett 1989). The length of lesions in *Banksia* correlated well with lengths predicted using previously determined growth temperature relationships. This is not the case in jarrah where growth is determined by water stress in addition to temperature. Tippett *et al.* (1987) found that trees that were well watered were more susceptible than those

suffering water stress. This was ascribed to the increased water content favouring growth of the pathogen in planta.

As indicated earlier, P. cinnamonii is considered to be a necrotrophic pathogen. Necrotrophic pathogens typically cause maceration of host tissue by bursting the cells releasing the intracellular contents on which they feed saprophytically. However, there have been a number of reports that P. cinuamomi does not always cause such symptoms. In a number of cases it can exist within the plant without the plant showing any adverse signs of infection. It is considered that under such conditions P. cinnamomi grows as a biotroph rather than as a necrotroph. This is not unusual as there are a number of examples of hemobiotriophic fungal pathogens that exhibit both types of lifestyles and can change from one to the other (Horbach et al. 2011). In the biotrophic mode P. cinnamonii appears to produce haustoria, which it uses to gain nutrients from the host (Crone et al. 2013).

In some cases after a hypha has penetrated the host cell wall, it may remain enveloped by a host-derived membrane, which appears as an invagination from the plasma membrane, and callose sheaths may be apposited onto this wall to encapsulate the invading hypha within the host cell (Jung et al. 2013). These callose sheaths called lignitubers vary in size and shape from simple spherical structures to complex branched lignitubers. The callose appositions may continue until the intracellular structure is completely encased. Callose layers are almost impermeable and, due to the incorporation of suberin, lignin and polyphenols, are highly resistant to enzymatic maceration. The elongated branched complex lignitubers have been observed in the cortex cells of the fine roots and root debris of both resistant and susceptible species. They have been found in 83% of root and root debris samples from E. marginata (resistant) and B. grandis (susceptible) in dieback sites (Jung et al. 2013). In samples from dieback-free sites short spherical lignitubers were observed occasionally, whilst no complex branched lignitubers were found. The involvement of lignitubers in the survival of P. cinnamomi is an open question. Complex lignitubers have been observed in root tissues of both E. marginata and B. graudis from which P. cinnamonii has been isolated after 6, 12, or 18 months dry air storage, and a lignituber from one B. grandis root sample has been observed to germinate giving rise to a chlamydospore (Jung et al. 2013).

IMPACT OF *PHYTOPHTHORA* ON THE ECOSYSTEM

Infestation of a site by *P. cinnamonii* leads to progressive death of susceptible species. However, these can take some time to die. Common flora in disease centres in the Esperance Plains Bioregion of Western Australia reached 50% mortality in five years (Shearer *et al.* 2007). This compares with more than six years for the two most common susceptible species on the Swan Coastal Plain. Eventually the susceptible species will be lost from the site. Since many of these are structurally dominant in the communities in which they occur, their removal has a dramatic effect on the community. Despite the removal of these species there is still sufficient pathogen inoculum present in symptomless or tolerant hosts to kill any

regenerating susceptible species, and thus the vegetation undergoes long-term changes in favour of less-susceptible species (Cahill *et al.* 2008).

A more immediate effect of infestation by P. cinnamomi is a reduction in canopy cover. Shearer et al. (2007) reported a 27-30% reduction in canopy cover in infested forest and woodland biomes in Western Australia compared to adjacent healthy vegetation. The reduction in canopy cover can lead to overexposure of understory species with adverse consequences. An example of this is the significant reduction in ground cover of the fern Lindsaea linearis in an infested Bauksia woodland compared to adjacent healthy woodland (Shearer et al. 2004a). As the fern is resistant to infection by P. cinuamonii, the effect was ascribed to increased exposure as a result of decreased canopy cover. Other plant species adversely affected by reduced canopy cover are Stylidium scandeus in the Stirling Ranges National Park in Western Australia (Wills 1993), and several other P. ciuuamonii resistant understory species in the jarrah forest (McDougall 2005).

Long-term monitoring of infested sites in Victoria has shown that at about 3-5 years post infestation fieldresistant sedges, rushes, grasses and volunteer weeds may colonise the infested site (Weste & Marks 1987). After about 15 years the original species have disappeared. After 22 years susceptible species begin to reappear (Dawson et al. 1985). In Western Australia, species richness decreased in old infested areas of the jarrah forest (Shearer et al. 2007). Similar changes were noted in infested Banksia woodland (Shearer & Hill 1989), but not in infested shrubland (Shearer et al. 2007). The reappearance and survival of susceptible species may be determined by the persistence of the pathogen at the site. It may persist for some considerable time, and under favourable conditions may erupt and infect recently arrived susceptible species leading to a new round of vegetation changes. In Victoria the pathogen could be recovered from infested sites 15 years after infestation but not after 20-30 years (Auesukaree et al. 2003). In contrast, in Western Australia P. ciunamomi could be isolated from infested sites in the jarrah forest 50 years after the initial infestation (McDougall et al. 2002). This survival is now recognised to be due to the ability of P. cinnamomi to colonise asymptomatic and symptomatic herbaceous perennials and annuals (Crone et al. 2012). Consequently, the pathogen is likely able to survive indefinitely in the absence of susceptible species.

The susceptibility of a species is not uniform but varies from site to site. Thus species such as Eucalyptus smithii, E. fastigata and E. fraxinoides are regarded as highly susceptible to P. cinuamonii in commercial plantations in South Africa yet none of these species is regarded as susceptible in native habitats (Cahill et al. 2008). Similarly Hibbertia hypericoides is highly susceptible to P. cinnamonii on the Swan Coastal Plain of Western Australia but of low susceptibility in the jarrah forest (Shearer & Dillon 1996). The basis of this site effect is not clear but may be related to the presence of P. cinuamomi suppressive microorganisms at some sites (Malacjzuk 1979), or to differences in the chemical nature of the soil. In Western Australia there is a negative correlation between soil calcium content and disease incidence (Stasikowski 2012). The presence of other plant species may also affect susceptibility: for example D'Souza et al. (2004) reported that Acacia species can protect adjacent plants of susceptible species such as Banksia grandis from infection. Resistance may also have a genetic component. Some native species show variation in susceptibility to P. cinnamomi with some varieties being quite resistant whereas others in the same species are more sensitive (Shearer et al. 2004a). This has also been described for a number of acacias, eucalypts, grasses, sedges, rushes and cereals (Weste & Marks 1987).

Changes in vegetation caused by Phytophthora dieback inevitably have an effect on the fauna that use the plants for cover, food or for nesting sites (Garkaklis et al. 2004). Comparative studies have shown lower numbers of invertebrates in infested sites (Nichols & Bamford 1985; Postle et al. 1986). Infested forest sites also supported fewer reptile and frog species compared to healthy forest sites (Nichols & Bamford 1985). Changes in vegetation also affect small mammal communities. Studies in the Brisbane Ranges in Victoria showed the abundance of Antechinus stuartii to be reduced in infested areas (Newell 1997). Studies in the coastal heathland at Anglesea in Victoria found that several small mammal species were also less abundant in infested coastal heathlands (S Laidlaw & B Wilson unpubl. data). A more recent study from Western Australia found that the abundance of the small marsupial, the yellow footed mardo (Antechinus flavipes leucogaster) was decreased in P. cinnamomi infested sites in the jarrah forest relative to non-infested sites (Armistead 2008). Another small marsupial whose habitat is negatively impacted by P. cinnamonii is the honeypossum (Tarsipes rostratus) (Dundas et al. 2013). The honeypossum feeds only on nectar and pollen and requires a high floristic diversity to maintain sustenance throughout the year. Of nine native plant species that are important in the diet of the honeypossum, five are susceptible to P. cinnamomi. The decreased abundance of faunal species will have ongoing effects on predatory species further up the food chain. Effectively their food sources will be diminished. In addition, as their habitat becomes more fragmented, animal populations will become more isolated and genetically less diverse. Eventually they will become too unstable.

SPREAD OF P. CINNAMOMI

Dispersal of P. cinnamomi is facilitated by moist or wet conditions and mild temperatures. The pathogen is dispersed in a variety of forms such as free zoospores in water, chlamydospores, oospores, stromata or lignitubers in soil or flowing water (Crone et al. 2012; Jung et al. 2013). It can also be dispersed in infected roots which can be moved along with the soil, or which grow from infested areas into adjacent non-infested areas (Shearer et al. 2004b). Therefore, any activity that causes disturbance of soil and increases water flow facilitates spread of the disease. Initially it was thought that soil disturbance was the cause of dieback because the disease occurred only at locations disturbed by activities such as mining, logging and road-building, but it was subsequently shown that such disturbance led to movement of infested soil and water and spread of the pathogen (Weste 1994). Prior to the demonstration that P. cinnamonii is responsible for the death of plants, gravel for roadbuilding was often unwittingly taken from infested to non-infested areas (Shearer & Tippett 1989). Propagules of *P. cinnamonii* can survive for up to 10 months in soil and gravel (Weste & Vithanage 1979). In the post-WWII period in Western Australia the increased frequency of road-building and mining activities was accompanied by an increase in the death of plants due to *P. cinnamonii* (Dell *et al.* 2005).

More recently the role of animals in the spread of *P*. cinnamomi has been investigated. Feral pigs are a major threat to the ecosystems in Western Australia. These animals roam over large areas and cause massive disturbance to the soil in their search for roots (Challies 1975; Department of Environment & Heritage 2005). These animals facilitate the spread of the disease in a number of ways: (i) they churn up huge volumes of soil bringing infested roots to the surface from where they can be more easily spread by other animals; (ii) they carry infested soil on their coats and on their trotters, sometimes for considerable distances; and (iii) the pathogen can survive passage through the pig digestive tract (Li et al. 2013). P. cinnamomi can also survive passage through the digestive tract of other animals such as birds and termites and thus these are potential vectors for disease spread (Keast & Walsh 1979).

MANAGEMENT OF PHYTOPHTHORA DISEASES

The aims of disease management are to reduce the effects of the pathogen in infested areas; and prevent its spread into non-infested areas. An integrated management program will consist of the following components: (i) chemical control; (ii) biological control; (iii) resistance breeding; and (iv) sanitary measures.

Chemical control

The most widely used chemical for control of oomycete pathogens is phosphite, an analogue of phosphate. Phosphite applied as an aerial spray, or as a trunk injection follows a sink-source relationship in the plant and accumulates in the roots (Guest et al. 1995). It prevents further colonisation of the plant by the pathogen, although it does not kill the pathogen and therefore needs to be re-applied periodically (Shearer & Fairman 1997). Foliar sprays are less effective than injections (Hardy et al. 2001). The percentage survival of Banksia baxteri and Lambertia inermis two years after a low-volume mist application was increased to 68% and 78%, compared to 31% and 54% in non-treated plants, respectively (Hardy et al. 2001). The effectiveness of phosphite application depends on the method of application, the dose applied, the plant species, the time of year it is applied (Hardy et al. 2001).

Biological control

Biological control involves the application of a bacterium or fungus or mixtures of microorganisms to plants with the result that they will protect the host plant from infection by pathogens. These biocontrol agents either colonise the internal tissues of the host plant as endophytes, or inhabit the zone around the root, the rhizoshpere: in some cases they do both. They protect the plant either by directly antagonising the pathogen, or by

enhancing the host's ability to ward off the infection (Ryan *et al.* 2008). The advantages of this approach are that it is non-toxic, and protection should be offered over a prolonged period, i.e. as long as the organism persists within the host. In addition because plants acquire their endophytes from adjacent plants (horizontal acquisition), this has the potential to offer protection to plants that appear after the application of the biocontrol agent (Arnold *et al.* 2003). Biocontrol is in essence, a self-perpetuating disease control system.

Soil microorganisms are known to be antagonistic to *P. cinnamomi* (Malajczuk 1983). Soils from sites in eastern and Western Australia where disease is minimal were found to contain a greater microbial load and a greater number of antagonistic bacteria and actinomycetes compared to sites where the disease was more developed. Reduced sporulation and increased hyphal lysis were observed in these soils. Malajczuk (1983) speculated that the antagonistic effect of bacteria may be due to the production of antibiotics that are active against *Phytophthora*.

Considerable effort has been expended to look for biological control agents of Phytophthora diseases in different crops (Table 2). Many studies report successful control using rhizobacteria, or endophytic bacteria or fungi. The impressive levels of disease control achieved in many of these studies are encouraging for the development of effective biological control strategies for P. cinnamomi in native ecosystems. However, considerable challenges remain as native ecosystems with a multiplicity of species are very different from horticultural or agricultural ecosystems with a single species for a limited time. One of these concerns is the duration of the protective effect. In their study on biocontrol of Phytophthora palmivora the agent of black pod disease in T. cacao by Trichoderma Hanada et al. (2009) found that the applied biocontrol agent had limited duration on the surface of the pods.

Resistance breeding

A number of native plant species show variability in susceptibility to *P. cinnamomi* in shadehouse tests which mirrors relative susceptibilities in natural environments indicating that there is a genetic basis for resistance

(Shearer et al. 2007). Some resistant lines of jarrah have been propagated by tissue culture and are being used for rehabilitation of diseased areas (McComb et al. 1994; Stukely & Crane 1994). Lines of Pinus radiata showing high levels of resistance to P. ciunamomi have been identified and are being used in the pine planting program (Butcher et al. 1984). However, using resistance for management of disease in natural environments is a long-term prospect as resistance sources of a great many species will need to be developed to replace those plants that are lost to disease. This strategy is complicated by the increased susceptibility of P. ciunamomi resistant lines to other pathogens (Shearer & Tippett 1989).

Sanitary measures

Sanitary measures involve reducing the spread of soil from infested to non-infested areas. This involves controlling access to infested areas so that infested soil is not inadvertently carried into non infested areas. One option used by the Western Australian State Government is to quarantine infested areas by closing roads and restricting access (Shearer & Tippett 1989). Where access cannot be totally restricted for commercial reasons such as logging or mining, measures such as vehicle washdown stations between infested and non-infested areas, and ensuring drainage runoff from road surfaces is diverted away from non-infested areas have been important factors in limiting the spread of the pathogen.

A critical component of sanitary measures is the ability to detect the pathogen so that infested areas can be accurately mapped and infested soil and water identified and prevented from moving into healthy areas. Traditionally methods such as baiting have been used for detection (O'Brien et al. 2009), although recent work with molecular methods suggests that it may give many false negative results. In their study of the distribution of *P. cinnamomi* across a disease front, Williams et al. (2009) reported that of 336 samples that tested positive for the presence of *P. cinnamomi* by PCR (polymerase chain reaction), only seven tested positive by baiting.

Recently Dunstan *et al.* (2010) evaluated measures to reduce the spread and to eradicate the pathogen from infected areas of Cape Riche on the south coast of Western Australia. The measures included removal of

Table 2 Biological control of Phytophthora diseases of different host species.

Crop species	Pathogen Antagonist P. capsici Serratia/Chromobacter/Lysobacter		% Disease control	Reference
Capsicum			81%	Kim et al. 2008
Red pepper	Phytophthora	B subtilis	86%	Lee et al. 2008
Capsicum	P. capsici	Rhizobacteria	_	Sang <i>et al.</i> 2011
Sweet pepper	P. capsici	Bacillus spp	80%	Sid <i>et al.</i> 2003
Asparagus	P. megasperma	Pseudomonas aureofaciens	55%	Godfrey et al. 2000
Strawberry	P. fragariae	Rhizobacteria	59%	Anandhakumar & Zeller 2008
Ornamental	P. ramorum	Trichoderma atroviridae	100%	Elliott et al. 2009
Pepper	P. capsici	Rhizosphere bacteria	83%	Mei <i>et al.</i> 2010
Pepper	P. capsici	Rhizobacteria	63%	Rajkumar et al. 2005
Avocado	P. cinnamomi	Endophytic bacteria and fungi	89%	Hakizimana et al. 2012
Apple	P. cactorum	Penicillium	73%	Alexander & Stewart 2001
Pepper	P. capsici	Rhizosphere bacteria	97%	Yuan et al. 2006
Cucumber	P. drechsleri	Rhizobacteria	85%	Maleki et al. 2011

vegetation either physically or by treatment with herbicides, surface and subsurface applications of fungicide and the installation of physical barriers to prevent root-to-root spread of the pathogen. The pathogen could not be detected at the site 6–9 months after application of these measures. It is considered that while the measures used here were drastic, they would be useful for treatment of spot infections that might further develop into wider infections.

CONCLUSIONS

P. cinnamomi continues to be a devastating pathogen. However, the application of molecular techniques to the study of P. cinnamomi in particular and to Phytophthora in general has greatly increased our understanding of the biology of the pathogen and how it persists and spreads. We have also been able to develop new and highly specific molecular tools for detection of P. cinnamomi in soil, water and plant tissue. We have developed more effective chemical treatments based on our increased understanding of how phosphite works. Other options for control such as biological control are still in the early stages of development. What are the prospects for the future? P. cinnamomi will always be with us. The best we can hope for is to effectively manage the disease and contain the pathogen. Critical for this is an understanding of the pathogen's biology and it is therefore crucial that research on the biology of the pathogen continues unabated. There are looming challenges with new questions: climate change, how will this affect the pathogen and its distribution? Other challenges are increases in the population of feral animals such as pigs as these lead to increased spread of the pathogen.

ACKNOWLEDGEMENTS

We would like to acknowledge the helpful comments from David Guest and Adrienne Hardham in preparation of this manuscript.

REFERENCES

- Alexander B J R & Stewart A 2001. Glasshouse screening for biological control agents of *Phytophthora cactorum* on apple (Mains domestica). New Zealand Journal of Crop and Horticultural Science 29, 159–169.
- Anandhakumar J & Zeller W 2008. Biological control of red stele (*Phytophthora fragariae* var. *fragariae*) and crown rot (*Pcactorum*) disease of strawberry with rhizobacteria. *Journal of Plant Diseases and Protection* 115, 49–56.
- Armistead R 2008. The impact of *Phytophthora cinnamomi* on the yellow-footed antechinus (mardo) (*Antechinns flavipes leucogaster*) (*Marsupialia: Dasynridae*). PhD thesis, Murdoch University, Murdoch (unpubl.).
- Arnold A E, Mejia L C, Kyllo D, Rojas E I, Maynard Z, Robbins N & Herre E A 2003. Fungal endophytes limit pathogen damage in a tropical tree. *Proceedings of the National Academy of Sciences* **100**, 15649–15654.
- Aussukaree C, Homma T, Kaneko Y & Harashima S 2003. Transcriptional regulation of phosphate-responsive genes in low-affinity phosphate-transporter-defective mutants in Saccharomyces cerevisiae. Biochemical and Biophysical Research Communications 306, 843–850.

- BEAKES G, GLOCKLING S & SEKIMOTO S 2012. The evolutionary phylogeny of the oomycete fungi. *Protoplasma* 249, 3–19.
- Brasier C M 1975. Stimulation of sex organ formation in *Phytophthora* by antagonistic species of *Trichoderma*. 1. The effect *in vitro*. *New Phytologist* 74, 183–194.
- Brasier C M 2008. The biosecurity threat to the UK and global environment from international trade in plants. *Plant Pathology* 57, 792–808.
- Burgess T I, Webster J L, Ciampini J A, White D, Hardy G E St J & Stukely M J C 2009. Re-evaluation of *Phytophthora* species isolated during 30 years of vegetation health surveys in Western Australia using molecular techniques. *Plant Disease* 93, 215–223.
- BUTCHER T B, STUKELY M J C & CHESTER G W 1984. Genetic variation in resistance of Pinus radiata to Phytophthora cinnamomi. Forest Ecology and Management 8, 197–220.
- CAHILL D M, ROOKES J E, WILSON B A, GIBSON L & McDougall K L 2008. Phytophthora cinnamomi and Australia's biodiversity: impacts, predictions and progress towards control. Anstralian Journal of Botany 56, 279–310.
- CHALLIES C N 1975. Feral pigs (Sus scrofa) on Auckland Island: status, and effects on vegetation and nesting sea birds. New Zealand Journal of Zoology 2, 479–490.
- CRONE M, McCOMB J A, O'BRIEN P A & HARDY G E ST J 2012. Survival of *Phytophthora ciunamomi* as oospores, stromata and thick-walled chlamydospores in roots of symptomatic and asymptomatic annual and herbaceous perennial species. *Fungal Biology* 117, 112–123.
- Crone M, McComb J A, O'Brien P A & Hardy G E St J 2013. Assessment of Australian native annual/herbaceous perennial plant species as asymptomatic or symptomatic hosts of *Phytophthora cinnamomi* under controlled conditions. Forest Pathology 43, 245–251.
- D'Souza N K, Colquidoun I J, Shearer B L & Hardy G E St J 2004. The potential of five Western Australian native Acacia species for biological control of *Phytophthora cinnamomi*. *Australian Journal of Botany* 52, 267–279.
- Davison E K, Stukeley M J C, Crane C E & Tay F C S 1994. Invasion of the phloem and xylem of woody stems and roots of Eucalyptus marginata and Pinus radiata by Phytophthora ciunamomi. Phytopathology 84, 335–340.
- DAWSON P, Weste G & Ashton D 1985. Regeneration of vegetation in the Brisbane Ranges after fire and infestation by *Phytophthora cinnamomi*. Australian Journal of Botany 33, 15–26.
- DEPARTMENT OF ENVIRONMENT AND HERITAGE 2005. Threat abatement plan for predation, habitat degradation, competition and disease transmission by feral pigs. http://www.environment.gov.au/system/files/resources/eddfe958-49e0-4c11-a994-68b113724b3a/files/feral-pig-tap.pdf
- Dell B, Hardy G E St J & Vear K 2005. History of *Phytophthora cinnamomi* management in Western Australia. *In:* Calver M C, Bigler-Cole H, Bolton G, Dargavel J, Gaynor A, Horwitz P, Mills J & Wardell-Johnston G (eds) *A Forest Conscienceness: Proceedings 6th National Conference of the Australian Forest History Society Inc.*, pp. 391–406. Millpress Science Publishers, Rotterdam
- Dobrowolski M P, Tommerup I C, Shearer B L & O'Brien P A 2003. Three clonal lineages of *Phytophthora cinnamomi* in Australia revealed by microsatellites. *Phytopathology* 93, 695–704
- Dundas S J, Fleming P A, Hardy G E St J 2013. Flower visitation by honey possums (*Tarsipes rostratus*) in a coastal banksia heathland infested with the plant pathogen *Phytophthora* ciunamomi, Australian Mammalogy 35, 166–174.
- Dunstan W A, Rudman T, Shearer B L, Moore N A, Paap T, Calver M C, Dell B & Hardy G E St J 2010. Containment and spot eradication of a highly destructive, invasive plant pathogen (*Phytophthora cinnamomi*) in natural ecosystems. *Biological Invasions* 12, 913–925.

- ELLIOTT M, SHAMOUN S F, SUMAMPONG G, JAMES D, MASRI S & VARGA A 2009. Evaluation of several commercial biocontrol products on European and North American populations of *Phytophthora ramorum*. *Biocontrol Science and Technology* 19, 1007–1021.
- ERWIN D C & RIBEIRO O K 1996. *Phytophthora* diseases worldwide. APS Press, St Paul.
- FRY W E, GOODWIN S B, MATUSZAK J M, SPIELMAN L J, MILGROOM M G & DRENTH A 1992. Population genetics and intercontinental migration of *Phytophthora infestans*. Annual Reviews of *Phytopathology* 30, 107–129.
- Godfrey S A C, Silby M W, Falloon P G & Mahanty H K 2000. Biological control of *Phytophthora megasperma* var. sojae, causal agent of *Phytophthora* rot of asparagus, by *Pseudomonas aureofaciens* PA147-2: a preliminary field trial. *New Zealand Journal of Crop and Horticultural Science* 28, 97–103.
- Garkaklis M J, Calver M C, Wilson B A & Hardy G E St J 2004. Habitat alteration caused by an introduced plant disease, *Phytophthora cinnamomi*: a potential threat to the conservation of Australian forest fauna. *In*: Lunney D J (ed.) *Conservation of Australia's Forest Fauna* (2nd edition), pp. 899–913. Royal Zoological Society of New South Wales, Mosman.
- GREGORY P H 1983. Some major epidemics caused by Phytophthora. In: Erwin D C, Bartnicki-Garcia S & Tsao P H (eds) Phytophthora: its biology, taxonomy, ecology, and pathology, pp. 271–278. American Phytopathological Society, St Paul.
- Guest D I, Pegg K G & Willey A W 1995. Control of Phytophthora diseases of tree crops using trunk injected phosphonates. Horticultural Reviews 17, 299–330.
- HAKIZIMANA J D, GRYZENHOUT M, COUTINHO T A & VAN DEN BERG N 2012. Root endophytes from *Persea americana* and their role against *Phytophthora cinnamoni* infection. *South African Journal of Botany* 79, 188–188.
- Hanada R E, Pomella A W V, Soberanis W, Loguercio L L & Pereira J O 2009. Biocontrol potential of *Trichodernia martiale* against the black-pod disease (*Phytophthora palmivora*) of cacao. *Biological Control* 50, 143–149.
- HANSEN E M 2008. Alien forest pathogens: Phytophthora species are changing world forests. Boreal Environment Research 13, 33–41.
- HARDHAM A R 2005. Phytophthora cinnamoni. Molecular Plant Pathology 6, 589-604.
- HARDY G E St J, BARRETT S & SHEARER B L 2001. The future of phosphite as a fungicide to control the soilborne plant pathogen *Phytophthora cinnamoni* in natural ecosystems. *Australasian Plant Pathology* 30, 133–139.
- HORBACH R, NAVARRO-QUESADA A R, KNOGGE W & DEISING H B 2011. When and how to kill a plant cell: infection strategies of plant pathogenic fungi. *Journal of Plant Physiology* 168, 51–62.
- JAYASEKERA A U, McComb J A, Shearer B L & Hardy G E St J 2007. In planta selfing and oospore production of Phytophthora cinnamomi in the presence of Acacia pulchella. Mycological Research 111, 355–362.
- JUNG T, COLQUHOUN I J & HARDY G E St J 2013. New insights into the survival strategy of the invasive soilborne pathogen Phytophthora cinnamoni in different natural ecosystems in Western Australia. Forest Pathology 43, 266–288.
- Keast D & Walsh L G 1979. Passage and survival of chlamydospores of *Phytophthora cinnamomi* Rands, the causal agent of forest dieback disease, through the gastrointestinal tracts of termites and wild birds. *Applied and Environmental Microbiology* 37, 661–664.
- Kim Y C, Jung H, Kim K Y & Park S K 2008, An effective biocontrol bioformulation against *Phytophthora* blight of pepper using growth mixtures of combined chitinolytic bacteria under different field conditions. *European Journal of Plant Pathology* 120, 373–382.
- Lee K J, Kamala-Kannan S, Sub H S, Seong C K & Lee G W 2008. Biological control of *Phytophthora* blight in red pepper

- (Capsicum annuum L.) using Bacillus subtilis. World Journal of Microbiology & Biotechnology 24, 1139–1145.
- Li A, WILLIAMS N, FENWICK S, HARDY G E ST J & ADAMS P 2013. Potential for dissemination of *Phytophthora cinnamomi* by feral pigs via ingestion of infected plant material. *Biological Invasions* 15, 1–10.
- MALACIZUK N 1979. Biological suppression of *Phytophthora* cinnamomi in eucalypts and avocado in Australia. *In*: Schippers B & Gams W (eds) *Soil-borne plant pathogens*, pp. 635–652. Academic Press, London.
- MALACJZUK N 1983. Microbial anatgonism to Phytophthora. In: Erwin D C, Bartnicki-Garcia S & Tsao P H (eds) Phytophthora: its biology, taxonomy, ecology and pathology, pp. 197–218. American Phytopathological Society, St Paul.
- MALEKI M, MOKHTARNEJAD L & MOSTAFAEE S 2011. Screening of rhizobacteria for biological control of cucumber root and crown rot caused by *Phytophthora drechsleri*. *Plant Pathology Journal* 27, 78–84.
- MBAKA J N, LOSENGE T, WAIGANJO M M & WAMOCHO L S 2010. Phenotypic variation in three Phytophthora cinnamomi populations from macadamia growing areas in Kenya. Journal of Animal & Plant Sciences 8, 900–911.
- McCarren K L, McComb J A, Shearer B L & Hardy G E St J 2005. The role of chlamydospores of *Phytophthora cinnamomi*—a review. *Australasian Plant Pathology* 34, 333–338.
- McComb J A, Stukely M & Bennet I 1994. Future ecosystems-use of genetic resistance. *In:* Withers P C, Cowling W A & Wills RT (eds) *Plant diseases in eucalypts: threats and impacts in southwestern Australia ecosystems*, pp. 179–180. Journal of the Royal Society of Western Australia 77.
- McDougall K L 2005. The responses of native Australian plant species to *Phytophthora cinnanuomi*. Appendix 4. Management of *Phytophthora cinnanuomi* for biodiversity conservation in Australia: Part 2. National best practice.
- McDougall K L, Hobbs R J & Hardy G E St J 2002. Vegetation of Phytophthora cinnanomi-infested and adjoining uninfested sites in the northern jarrah (Eucalyptus marginata) forest of Western Australia. Australian Journal of Botany 50, 277–288.
- Mei X L, Zhao Q Y, Tan S Y, Xu Y C, Shen B & Shen Q R 2010. Screening, identification, and biocontrol effect of antagonistic bacteria against *Phytophthora capsici*. *Chinese Journal of Applied Ecology* 21, 2652–2658.
- MIRCETICH S M & ZENTMEYER G A 1966. Production of oospores and chlamydospores of *Phytophthora cirmamomi* in roots and soil. *Phytopathology* **56**, 1076–1078.
- Newell G R 1997. The abundance of ground-dwelling invertebrates in a Victorian forest affected by dieback (*Phytophthora cinnamomi*) disease. *Australian Journal of Ecology* 22, 206–217.
- Nichols O G & Bamford M J 1985. Reptile and frog utilisation of rehabilitated bauxite minesites and dieback affected sites in Western Australia's Jarrah Encalyptus marginata forest. Biological Conservation 34, 227–249.
- O'BRIEN P A, WILLIAMS N & HARDY G E ST J 2009. Detecting Phytophthora. Critical Reviews in Microbiology 35, 165–181.
- OLD K M, Dudzinski M J & Bell J C 1988. Isozyme variability in field populations of *Phytophthora cinnamomi* in Australia. *Australian Journal of Botany* 36, 355–360.
- PODGER F D, DOEPEL R F & ZENTMYER G A 1965. Association of *Phytophthora cinnamomi* with a disease of *Eucalyptus marginata* forest in Western Australia. *Plant Disease Reporter* 49, 943–947.
- Postle A C, Majer J D & Bell D T 1986. Soil and litter invertebrates and litter decomposition in Jarrah (Eucalyptus marginata) forest affected by Jarrah dieback fungus (Phytophthora cinnamomi). Pedobiologia 29, 47–69.
- RAJKUMAR M, LEE W H & LEE K J 2005. Screening of bacterial antagonists for biological control of *Phytophthora* blight of pepper. *Journal of Basic Microbiology* 45, 55–63.
- RYAN R P, GERMAINE K, FRANKS A, RYAN D J & DOWLING D N 2008.

- Bacterial endophytes: recent developments and applications. *FEMS Microbiology Letters* **278**, 1–9.
- SANG M K, KIM J D, KIM B S & KIM K D 2011. Root treatment with rhizobacteria antagonistic to *Phytophthora* blight affects anthracnose occurrence, ripening, and yield of pepper fruit in the plastic house and field. *Phytopathology* 101, 666–678.
- Scott P, Burgess T I & Hardy G E St J 2013. Globalization and *Phytophthora*. *In*: Lamour K (ed.) *Phytophthora a global perspective*, pp. 226–233. CABI, Wallingford.
- Scott P M, Burgess T I, Barber P A, Shearer B L, Stukely M J C, Hardy G E St J & Jung T 2009. *Phytophthora multivora* sp. nov., a new species recovered from declining *Eucalyptus, Banksia, Agonis* and other plant species in Western Australia. *Personia* 22, 1–13.
- Shea S R & Broadbent P 1983. Developments in cultural and biological control of *Phytophthora* diseases. *In:* Erwin D C, Bartnicki-Garcia S & Tsao PH (eds) *Phytophthora: its biology, taxonomy, ecology and pathology*, pp. 335–350. American Phytopathological Society, St Paul.
- SHEARER B L, CRANE C E, BARRETT S & COCHRANE A 2007. Phytophthora cinnamomi invasion, a major threatening process to conservation of flora diversity in the South-West Botanical Province of Western Australia. Australian Journal of Botany 55, 225–238.
- Shearer B, Crane C & Cochrane A 2004a. Quantification of the susceptibility of the native flora of the South-West Botanical Province, Western Australia, to *Phytophthora cinnamomi*. *Australian Journal of Botany* **52**, 435–443.
- SHEARER B L, CRANE C E & FAIRMAN R G 2004b. Phosphite reduces disease extension of a *Phytophthora cinnamomi* front in Banksia woodland, even after fire. *Australasian Plant Pathology* 33, 249–254.
- Shearer B L & Dillon M 1996. Susceptibility of plant species in banksia woodland on the swan coastal plain Western Australia to infection by *Phytophthora cinnamonii*. Australian Journal of Botany 44, 433–445.
- Shearer B L & Fairman R G 1997. Phosphite inhibits lesion development of *Phytophthora cinnamomi* for at least four years following trunk injection of *Bauksia* species and *Eucalyptus marginata*. In: Tommerup I & Burgess T (eds) *Programme and Summaries: Australasian Plant Pathology Society, 11th Biennial Conference: Perth,* p. 181.
- SHEARER B L & HILL T C 1989. Diseases of Banksia woodlands on the Bassendean and Spearwood dune systems. Journal of the Royal Society of Western Australia 71, 113–114.
- SHEARER B L & TIPPETT J T 1989. Jarrah dieback: the dynamics and management of Phytophthora cinnamomi in the jarrah (Eucalyptus marginata) forest of south-western Australia. Department of Conservation and Land Management Research Bulletin 3.
- SID A, EZZIYYANI M, EGEA-GILABERT C & CANDELA M E 2003. Selecting bacterial strains for use in the biocontrol of diseases

- caused by Phytophthora capsici and Alternaria alternata in sweet pepper plants. Biologia Plantarum 47, 569–574.
- STASIKOWSKI P 2012. Biochemical effects of phosphite on the phytopathogenicity of *Phytophthora cinnamomi* Rands. PhD thesis, Murdoch University, Murdoch (unpubl.).
- Stukely M J C & Crane C E 1994. Genetically based resistance of Encalyptus marginata to Phytophthora cinnamomi. Phytopathology 84, 650-656.
- TIPPETT J T, CROMBIE D S & HILL T C 1987. The effect of phloem water relations on the growth of *Phytophthora ciunamomi* in *Eucalyptus marginata*. *Phytopathology* 77, 246–250.
- Tyler B M, Tripathy S, Zhang X G, Dehal P, Jiang R H Y, Aerts A, Arredondo F D, Baxter L, Bensasson D, Beynon J L, Chapman J, Damasceno C M B, Dorrance A E, Dou D, Dickerman A W, Dubchak I L, Garbelotto M, Gijzen M, Gordon S G, Govers F, Grunwald N J, Huang W, Ivors K L, Jones R W, Kamoun S, Krampis K, Lamour K H, Lee M-K, McDonald W H, Medina M, Meijer H J G, Nordberg E K, MaClean D J, Ospina-Giraldo M D, Morris P F, Phuntumart V, Putnam N H, Rash S, Rose J K C, Sakihama Y, Salamov A A, Savidor A, Scheuring C F, Smith B M, Sobral B W S, Terry A, Torto-Alalibo T A, Win J, Xu Z, Zhang H, Grigoriev I V, Rokhsar D S & J L 2006. *Phytophthora* genome sequences uncover evolutionary origins and mechanisms of disease. *Science* 313, 1261–1266.
- Weste G 1994. Impact of *Phytophthora* species on native vegetation of Australia and Papua New Guinea. *Australasian Plant Pathology* 23, 190–209.
- Weste G & Marks G C 1987. The biology of Phytophthora cinnamomi in Australian forests. Annual Review of Phytopathology 25, 207–229.
- Weste G & Vithanage K 1979. Survival of chlamydospores of Phytophthora ciunamomi in several non-sterile host-free forest soils and gravels at different soil water potentials. Australian Journal of Botany 27, 1–9.
- WILLIAMS N, HARDY G E ST J & O'BRIEN P A 2009. Analysis of the distribution of *Phytophthora cinnamomi* in soil at a disease site in Western Australia using nested-PCR. *Forest Pathology* 39, 95–109.
- Wills R T 1993. The ecological impact of *Phytophthora cinnamomi* in the Stirling Range National Park, Western Australia. *Australian Journal of Ecology* 18, 145–155.
- Yuan S, Zhou M, Yuan S Z & Zhou M G 2006. Screening and root colonization of biocontrol agents against *Phytophthora capsici*. *Journal of Yangzhou University, Agricultural and Life Sciences Edition* 27, 93–97.
- ZENTMYER G A 1979. Stimulation of sexual reproduction the A2 mating type of *Phytophthora cinnamomi* by a substance in avocado roots. *Phytopathology* **69**, 1129–1131.

Received 2 October 2013; accepted 22 February 2014



Arachnida (Arthropoda: Chelicerata) of Western Australia: overview and prospects

M S HARVEY*

Department of Terrestrial Zoology, Western Australian Museum, Locked Bag 49, Welshpool DC, WA 6986, Australia. Mark.harvey@museum.wa.gov.au.

The history of the study of arachnids (spiders, scorpions, ticks, mites and their relatives) in Western Australia is briefly reviewed, and the main periods of activity are documented: 1860s–1910s, between the wars, after World War II, and the modern era. The fauna consists of at least 1400 named species (but the mite fauna is imperfectly documented), and it is estimated that ~6000 species exist, the majority of which are currently undescribed

KEYWORDS: history, pseudoscorpions, scorpions, spiders, taxonomy.

INTRODUCTION

The arachnid fauna of Western Australia represents a fascinating tableau of ancient relictual species and more recently arrived invaders. While the spiders (order Araneae) and mites (superorder Acari) are numerically dominant, representatives of six other orders—Scorpiones, Pseudoscorpiones, Opiliones, Schizomida, Amblypygi and Palpigradi (Figure 1)—have been found in the state. The size of the fauna is unknown, but certainly comprises several thousand species, the majority of which are undescribed and lack valid scientific names.

The history of discovery of the arachnid fauna of the region can be conveniently divided into four time periods: 1860s–1910s, between the wars, after WWII, and the Modern Era, and I here present a brief overview of the major researchers and their areas of expertise.

1860s-1910s

The first arachnids to be described from specimens explicitly collected in Western Australia were various trap-door spiders collected in 'Swan River' or 'West Australia' and studied by Oliver Pickard-Cambridge (1828–1917: usually cited as O P-Cambridge by the arachnological community), an English clergyman and zoologist based in Bloxworth, England. The first species to be named were the trap-door spiders *Eriodon granulosum* and *E. crassum* by Cambridge (1869). Both specimens were taken from 'Swan River' which at the time referred to the Swan River Colony. *Eriodon granulosum* was based on a single male, and *E. crassum* was based on a female, and it took nearly 80 years before they were recognised as the same species which is

nowadays known as Missulena granulosum (Cambridge). This species is quite common throughout southwestern Australia where it persists in woodland habitats. The next arachnid to be described was Idiops blackwalli Cambridge (1870) based on an adult male collected from Swan River. The species was quickly transferred to a new genus by Ausserer (1871). Idiommata blackwalli is a large, impressive species still common in the Perth region. The trapdoor spiders Aganippe latior (based on a female from 'West Australia'), Eriodon insignis (based on a male from Swan River), and E. incertus (a male from Swan River) were also described by Cambridge, but in 1877 (Cambridge 1877). Unfortunately, there is little background information regarding how the specimens came to be sent to England as the name of the collector of the specimens was not mentioned by Cambridge in his

During the exploration by the British settlers, natural history specimens started to trickle back to England, where many different arachnids were studied by local scientists keen to document the fauna of the world. Specimens were also being sent to the Australian Museum in Sydney where spider expert William J Rainbow (1856–1919) was documenting many new species of different families. Some notable additions to the Western Australian arachnid fauna of the time included studies on scorpions (Pocock 1891, 1898, 1902) and spiders (Hogg 1914; Rainbow 1914; Rainbow & Pulleine 1918).

Around the turn of the 20th century European museums were funding scientists to visit various parts of the world to amass scientific collections to better understand the world's biota. The Michaelsen-Hartmeyer expedition to southwestern Australia was typical of the time, with two distinguished German scientists traveling to far-flung corners of the globe to document the biota of a region and to bring specimens back for their institutional scientists and colleagues to study. Wilhelm Michaelsen (1860-1937) and Robert Hartmeyer (1874-1923) stayed in Western Australia for several months in 1905 and travelled as far north as Shark Bay, south to Albany and east to Kalgoorlie and Norseman (Michaelsen & Hartmeyer 1907-1908), collecting in both terrestrial and marine habitats. The then Director of the Museum, Bernard H Woodward

^{*} Research Associate, Division of Invertebrate Zoology, American Museum of Natural History, New York, USA, and Department of Entomology, California Academy of Sciences, San Francisco, California, USA; School of Animal Biology, University of Western Australia, Crawley, WA 6009, Australia; School of Natural Sciences, Edith Cowan University, Joondalup, WA 6027, Australia.

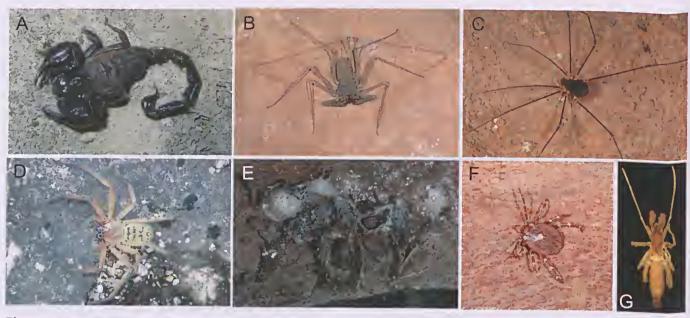


Figure 1 Representative orders of Western Australian Arachnida. (a) Scorpiones, *Urodacus butleri* Volschenk, Harvey and Prendini. (b) Amblypygi, *Charon* sp.. (c) Opiliones, *Dampetrus* sp.. (d) Araneae, *Delena lapidicola* (Hirst). (e) *Synsphyronus apimelus* Harvey. (f) Acarina, *Amblyomna triguttatum* L. Koch. (g) Schizomida, *Paradraculoides bythius* Harvey, Berry, Edward & Humphreys. Images by Western Australian Museum.

lamented that the Western Australian government had supplied funds and equipment to assist the German expedition, but provided little in the way of assistance to the fledging Museum. Michaelsen and Hartmeyer dispatched specimens collected during their journey to a variety of European colleagues, all specialists in their discipline. Several arachnid groups were treated by taxonomists, and the most important contribution was the section on spiders published in two parts by the eminent French spider expert Eugène Simon who was based at the Muséum national d'Histoire naturelle, Paris (Simon 1908, 1909). In these papers he described 160 new species and 21 new genera. The specimens were divided between the museums of Berlin, Hamburg and Paris, with a few specimens sent to the Western Australian Museum (Main & Harvey 1992). Despite their value as type specimens, the Western Australian Museum specimens were removed from ethanol and mounted on pins; they were then displayed in the public gallery of the museum for many years. They have since been returned to ethanol and stored amongst the research collections of the museum (Main & Harvey 1992). Three other arachnid groups collected during the Michaelsen-Hartmeyer expedition were studied by taxonomists. The scorpions were examined by Karl Kraepelin who recorded several different species, including several new species (Kraepelin 1908). Albert Tullgren, a Swedish scientist who specialised in the study of arachnids, examined the few pseudoscorpions collected by the German pair (Tullgren 1909). He described three new species. Lohmann (1909) worked on the marine mites, of which very few were collected.

The Swedish zoologist and ethnographer Eric Georg Mjöberg (1882–1938) also visited Western Australia, making pioneering collections in the Kimberley. The only arachnids that were documented from that collection were the scorpions (Kraepelin 1916).

BETWEEN THE WARS

Ludwig Glauert

Ludwig Glauert (1879–1963) (Figure 2a) was born in Yorkshire, England and trained as a geologist before emigrating to Perth in 1908. He was appointed to the Western Australian Museum in 1910 after a short stint with the Geological Survey of Western Australia. He led the museum as Keeper of the Biological Collections after his return from service in World War I in 1920. This title was altered to Curator in 1927 and to Director in 1954.

Although responsible for building the collections of the fledging Western Australian Museum, Glauert was also responsible for the very first arachnids to be described from Western Australia by a person resident in the state. He described several species of marbled scorpions of the family Buthidae from Australia (Glauert 1925), including Lychas jonesae from the Goldfields region of Western Australia. In this seminal paper, he also described several species from other parts of Australia. The type specimen of L. jonesae was based on a specimen lodged in the collection of the Western Australian Museum, where it resides to this day. Although his 1925 paper was tantalizingly titled 'Australian Scorpionidea. Part 1', subsequent parts in this series were never published even though he was working on scorpion manuscripts up until his death in 1963 (Serventy 1963). These were published posthumously in 1963, one containing the description of a remarkable new species of Urodacus from the Canning Stock Route (Glauert 1963b), and the other consisting of a list of Western Australian scorpions (Glauert 1963a).

Glauert maintained correspondence with prominent arachnologists of the time and was responsible for dispatching harvestmen specimens on loan to two specialists, who published the results of their studies. The

German Carl-Friedrich Roewer (1881–1963) was a world-renowned and prolific specialist who published on the samples sent to him by Glauert (Roewer 1929), including the new genus and species, *Bindoona glauerti* Roewer, 1929. The genus was named in honour of the town of Bindoon, from where the specimens had been collected, and the species was named, of course, in honour of Glauert. Glauert also lent harvestmen specimens to the young and energetic New Zealand arachnologist Raymond Forster (1922–2000), who published the results of his study in 1952 (Forster 1952). The most important species was yet another new genus and species, *Dingupa glauerti*, this time named for the small hamlet of Dingup, but also for the collector.

Herbert Womersley (1889–1962) was born in Lancashire and moved to Australia with his wife and children in 1930 to take up a three-year post with the Division of Economic Entomology (C S & I R, later to become CSIRO) to study the distribution and control of two introduced pests, clover springtail [Sminthurus viridis (Linnaeus)] and the red-legged earth mite [Halotydeus destructor (Tucker)]. Due to the financial difficulties facing organisations such as C S & I R during the Great Depression, Womersley left Western Australia and joined the South Australian Museum in 1933. He worked there for the rest of his professional life until his retirement in 1959, first as Entomologist, and after 1954 as Acarologist.

While living in Perth, Womersley befriended a young entomologist Duncan Campbell Swan (1907-1960), who was born in Perth and who studied at the University of Western Australia, and received a Master of Science degree at the University of Adelaide in 1935. After serving in the Medical Unit of the Royal Australian Air Force during World War II, Swan became head of the Department of Entomology at the Waite Institute in Adelaide, South Australia (Prescott & Brookes 1961). Swan became a renowned medical and agricultural entomologist, but he holds the honour of being the first person born in Western Australia to describe a new Western Australian arachnid. Furthermore, this description was only the second arachnid to be named by a resident of Western Australia, after Lychas jonesae. Swan described a new species of tick, Ixodes Inydromyidis (Swan 1931), which had been collected from a water rat (Hydromys fuliginosus) and a black rat (Rattus rattus) in the hills near Perth. Quite fittingly, the specimens from

Hydromys had been collected by Ludwig Glauert, demonstrating his considerable skills in promoting the study of the Western Australian fauna. Swan's holotype specimen is lodged in the Western Australian Museum.

There appears to be relatively little other arachnological activity during this time, apart from the description of some new Western Australian mites (Hirst 1928).

AFTER WORLD WAR II

Barbara York Main

Barbara York (Figure 2b) was born in 1929 and grew up on the family farm at Tammin, in the heart of Western Australia's wheatbelt. After correspondence classes organised through the Western Australian Education Department under the tutelage of her mother, a former teacher, she was awarded a scholarship to Northam High School. She entered the University of Western Australia in 1947 and graduated with an Honours degree in Science, majoring in Zoology in 1950. During classes at the university she met her future husband, Albert (Bert) Main (1919-2009), a returned serviceman who was imprisoned in Europe during World War II. Her PhD was awarded by the University in 1956 for a thesis studying aganippine trapdoor spiders, which formed the basis of a paper published the following year (Main 1957). Since then she has produced a steady stream of publications devoted to the biology, natural history and taxonomy of spiders, particularly mygalomorph spiders (e.g. Main 1985, 1993, 2001b; Main & Framenau 2009; Mason et al. 2013). Her first scientific paper (Main 1952) included the description of two new species of the trapdoor spider genus Idiosoma, representing only the second and third arachnid species to be named by someone born in Western Australia.

She has also contributed papers on the biogeography of the region (Main 1991, 1998, 1999, 2001a; Main *et al.* 2000), and strongly promoted the conservation of spiders and other 'forgotten' invertebrates. Her books on natural history, including *Between Wodjil and Tor* (Main 1967) and *Spiders* (Main 1976, 1984), have received national acclaim. Further details of Barbara's life and career are provided by Hodgkin (1995).



Figure 2 (a) Ludwig Glauert. (b) Barbara York Main. (c) Lucien E Koch. Images by Western Australian Museum.

Her first post-graduate student, Michael Gray, completed his Master of Science thesis in 1968 at the University of Western Australia entitled 'Comparison of three genera of trapdoor spiders (Ctenizidae, Aganippini) with respect to survival under arid conditions'. He went on to become Curator of Arachnids at the Australian Museum in Sydney, retiring in 2005.

The high regard in which Barbara Main is held amongst invertebrate systematists is that she has had more than 20 species named in her honour, including 13 spiders, as well as several genera including the spiders *Bymainiella* Raven (Raven 1978) and *Mainosa* Framenau (Framenau 2006), and the pseudoscorpion *Barbaraella* Harvey (Harvey 1995a).

Lucien Everard Koch

Lucien Koch (Figure 2c) was born in 1932 in Colombo, Sri Lanka (then Ceylon) where he completed his early education followed by tertiary education at the University of Western Australia. After a short stint from 1955 at the Department of Agriculture, he transferred to the Western Australian Museum where he was Curator of Entomology which at the time also encompassed the field of arachnology. His role altered to Curator of Arachnology with the appointment of an entomologist in 1980.

His arachnological research focused on the Australian scorpion fauna (Koch 1963, 1970, 1978, 1981), culminating in a systematic review of the scorpions of the entire region in which he described seven new species (Koch 1977). This body of work formed the basis for his PhD which he received from the University of Reading, United Kingdom, under the supervision of W D L Ride (1926–2011), who was at the time Director of the Western Australian Museum. Koch also published a review of the scolopendrid centipedes of Australia (Koch 1983a, b; Koch & Colless 1986), stabilising the identity of these iconic invertebrate predators. He retired from the Museum in 1987.

MODERN ERA

Graeme Talbot Smith (1938–1999) joined the CSIRO Division of Wildlife Research in Perth in 1974 where he spent nearly 20 years studying birds, mammals and scorpions. His ecological research on Western scorpions led to several important publications (Abensperg-Traun & Smith 1999; Smith 1990, 1998; Smith & McKenzie 2000) and he also contributed to the description of a new species of *Urodacus* from the Shark Bay region (Volschenk *et al.* 2000). He retired in 1993, and after his death six years later, his collection was transferred to the Western Australian Museum.

Western Australian spiders were also studied by an unlikely source, the Western Australian Museum's Assistant in the fish section, Roland (Roly) J McKay, who commenced employment in 1964. He began a revision of the Australian wolf spiders in 1968, initially using Barbara Main's large collection and notes (McKay 1973). By the time he published his first paper (McKay 1973), he had transferred to Brisbane as the Curator of Fishes at the Queensland Museum. He eventually published 15 papers over a 13 year span with his final contributions in 1985 (McKay 1985a, b).

During Lucien Koch's curatorship, Julianne Waldock was appointed as technical officer in the arachnology section of the Western Australian Museum in 1982, a post she still holds. She studied at the University of Western Australia, and has published descriptions of several new species (Waldock 1995, 2009; Żabka & Waldock 2012).

William (Bill) F Humphreys started employment at the Western Australian Museum in 1980 after studying in England, completing a PhD at the Australian National University, Canberra and a postdoctoral appointment at La Trobe University. Although originally employed as part of the Biogeography and Ecology section of the museum, he devoted part of his research program to the study of the surface structure of the eggs of chelicerates, particularly spiders (Humphreys 1983, 1987, 1995). He later turned his attention to the study of troglobitic animals, in particular the schizomid Schizomus vinei Harvey [later to become Draculoides vinei (Harvey)], partly based on data collected by Brian Vine in the relatively unexplored caves of the Cape Range region (Humphreys 1990; Humphreys et al. 1989; Vine et al. 1988). This work led to the discovery of high biological diversity in many different subterranean ecosystems throughout Western Australia, including the discovery and detailed documentation of many arachnids (Harvey & Humphreys 1995; Humphreys 1993, 2001).

After L E Koch's retirement, Mark Harvey was appointed Curator of Arachnids at the Western Australian Museum in 1989, after completing his PhD at Monash University in 1983 and postdoctoral appointments at the Division of Entomology, Canberra and the Museum of Victoria, Melbourne. He has mentored several postgraduate students and postdoctoral arachnological researchers at the Museum and via collaborative links with local universities, including Erich Volschenk (scorpions), Karen Edward (millipedes and spiders), Volker Framenau (spiders), Christopher Taylor (harvestmen), Danilo Harms (spiders pseudoscorpions) and Michael Rix (spiders). He has published numerous papers on the arachnid fauna of Western Australia and elsewhere, and described many new arachnid species often in collaboration with his research team, belonging to several different orders including pseudoscorpions (Harvey 2012; Harvey & Edward 2007; Harvey & Leng 2008; Harvey & Volschenk 2007), spiders (Harvey 1995b, 2002), scorpions (Volschenk et al. 2012; Volschenk et al. 2000), schizomids (Harvey 1988, 2001; Harvey et al. 2008), water mites (Harvey 1996, 1998a, b) and palpigrades (Barranco & Harvey 2008).

Arachnids have also featured heavily in wide-scale biological surveys of significant sections of the state to gain a better idea of biotic assemblages and their conservation needs. These include surveys of the Kimberley rainforests (McKenzie *et al.* 1991), southern Carnarvon Basin (Burbidge *et al.* 2000), the Agricultural Zone and Wheatbelt (Keighery *et al.* 2004) and the Pilbara (George *et al.* 2009). These surveys have also been complemented by more localised studies of spider assemblages including the southwest forests (Brennan *et al.* 2004a, b) and the arid zone (Langlands *et al.* 2006, 2010).

Table 1 Numbers of named arachnid species collected in Western Australia, based on specimens lodged in the Western Australian Museum.

Order	Named species (indigenous)	Introduced species	Total	Comments
Acari			The taxon "Acari" is used in the broadest sense; see Krantz & Walter (2009) for alternative classification	
Amblypygi	0	0	0	An undescribed species of whip spiders has been recently recorded from northern Western Australia (Harvey <i>et al.</i> 2012b)
Araneae	860	18	878	<u> </u>
Opiliones	24	0	24	_
Palpigradi	1	1	2	_
Pseudoscorpiones	79	2	81	_
Schizomida	14	0	14	_
Scorpiones	29	0	29	_
Totals	1407	22	1429	_

THE FUTURE

The Western Australian arachnid fauna is moderately diverse, with more than 1400 named indigenous species represented in the collections of the Western Australian Museum (Table 1). This figure is an underestimate of the entire fauna as specimens of many species, especially mites, are not represented in the Western Australian Museum collections. However, this figure is relatively accurate for the other orders. There are also several notable introduced species, including the pests redlegged earth mite (Halotydeus destructor) and cattle tick (Rhipicephalus microplus); the spider families Agelenidae, Oecobiidae, Scytodidae and Sicariidae are only represented by introduced species.

The total extent of the arachnid fauna of Western Australia is difficult to estimate, as new species are continually being recognised and documented, but the lag-time until the species is formally named can be extensive. This masks the overall diversity of the group.

An estimate of ~6000 species would not be unreasonable, with ~3500 mite species, 2000 spiders and ~500 species of the smaller orders.

The majority of arachnological research in Western Australia over the past 150 years has been focused on taxonomy in an attempt to document the fauna of the state. The success of that progress can be graphically portrayed (Figure 3), depicting the 722 species named until 2012 for which the primary types are lodged in the Western Australian Museum. This includes 405 spiders, 262 mites and ticks, 36 pseudoscorpions, 15 harvestmen, 14 schizomids, 9 scorpions and 1 palpigrade. Of course, many more species have been described for which the primary types are lodged in other institutions, either nationally or internationally.

While the taxonomic results of the scientific research on arachnids has usually taken the form of papers published in scientific journals, there are growing efforts to deliver online content in the form of web-based

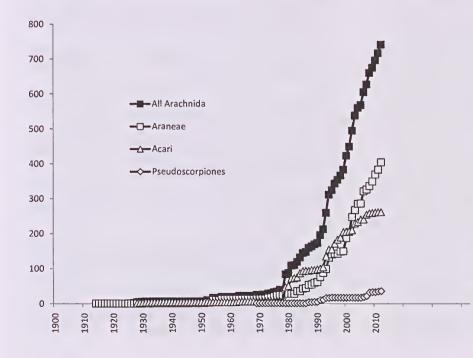


Figure 3 Graph showing primary types (holotypes, lectotypes and neotypes) of Arachnida in the Western Australian Museum collection 1914–2012, showing rapid growth in the documentation and description of new species since the 1980s.

identification guides (e.g. WAMinals – see http://museum.wa.gov.au/catalogues/waminals/about-waminals). Spatial data concerning individual arachnid species are also aggregated by different portals including the Atlas of Living Australia (see http://www.ala.org.au/), Online Zoological Collections of Australian Museums (see http://www.ozcam.org.au/) and NatureMap (see http://naturemap.dec.wa.gov.au/default.aspx). These portals provide comprehensive and up-to-date data on the Australian biota to assist managers, ecologists and taxonomists pursue their goals.

A relatively new form of biodiversity documentation has been the recent advent of molecular-sequencing techniques. This method assists in species-level identifications and can provide data on the evolutionary history and relationships within clades. Some notable recent publications with DNA sequence data of Western Australian arachnids include the characterisation of new species of spiders (Harms & Framenau 2013; Harvey et al. 2012a; Rix & Harvey 2012; Rix et al. 2010) and schizomids (Harvey et al. 2008). These modern techniques, when combined with traditional taxonomic descriptions, are slowly combining to form a reasonably comprehensive view of the Western Australian arachnid fauna, providing assistance to managers, biodiversity professionals and ecologists of the significance of the iconic organisms in the Western Australian landscape.

ACKNOWLEDGEMENTS

I am very grateful to Julianne Waldock for providing some of the information for this article, and to her, Barbara Main and Michael Rix for comments on a draft of the manuscript.

REFERENCES

- ABENSPERG-TRAUN M & SMITH G T 1999. How small is too small for small animals? Four terrestrial arthropod species in different-sized remnant woodlands in agricultural Western Australia. *Biodiversity and Conservation* 8, 709–726.
- Ausserer A 1871. Beiträge zur Kenntniss der Arachniden Familie der Territelariae Thorell (Mygalidae). Verhaudlungen der Zoologisch-Botanischen Gesellschaft in Wien 21, 117–224.
- Barranco P & Harvey M S 2008. The first indigenous palpigrade from Australia: a new species of *Eukoenenia* (Palpigradi: Eukoeneniidae). *Invertebrate Systematics* 22, 227–233.
- Brennan K E C, Moir M L & Majer J D 2004a. Conservation and biodiversity of spiders in Western Australian jarrah forest: untangling multiple disturbance effects from burning and mining. In: Lunney D (ed.) Conservation of Australia's Forest Fanna, pp. 914–935. Royal Zoological Society of New South Wales, Mossman.
- Brennan K E C, Moir M L & Majer J D 2004b. Exhaustive sampling in a Southern Hemisphere global biodiversity hotspot: inventorying species richness and assessing endemicity of the little known jarrah forest spiders. *Pacific Conservation Biology* 10, 241–260.
- Burbidge A H, Harvey M S & McKenzie N L 2000. Biodiversity of the southern Carnarvon Basin. Records of the Western Australian Museum, Supplement 61,
- Cambridge O P- 1869. Descriptions of a new genus and six new species of spiders. *Journal of the Linnean Society of London* 10, 264–276.
- CAMBRIDGE O P- 1870. Supplementary notice on the genus Idiops. Proceedings of the Zoological Society of London 1870, 152–157.

- Cambridge O P- 1877. On some new genera and species of Araneida. Annals and Magazine of Natural History (4)19, 26–39.
- FORSTER R R 1952. Western Australian Opiliones. *Journal of the Royal Society of Western Australia* 36, 23–29.
- Framenau V W 2006. *Mainosa*, a new genus for the Australian "shuttlecock wolf spider". *Journal of Arachuology* 34, 206–213.
- GEORGE A S, McKenzie N L & Doughty P 2009. A Biodiversity Survey of the Pilbara Region of Western Australia, 2002– 2007. Records of the Western Australian Museum, Supplement 78.
- GLAUERT L 1925. Australian Scorpionidea. Part 1. Journal of the Royal Society of Western Australia 11, 89–118.
- GLAUERT L 1963a. Check list of Western Australian scorpions. Western Australian Naturalist 8, 181–185.
- GLAUERT L 1963b. Notes on *Urodacus* scorpions. Western Australian Naturalist 8, 132-135.
- Harms D & Framenau V W 2013. New species of mouse spiders (Araneae: Mygalomorphae: Actinopodidae: *Missulena*) from the Pilbara region, Western Australia. *Zootaxa* 3637, 521–540.
- HARVEY F S B, FRAMENAU V W, WOJCIESZEK J M, RIX M G & HARVEY M S 2012a. Molecular and morphological characterisation of new species in the trapdoor spider genus *Auame* (Araneae: Mygalomorphae: Nemesiidae) from the Pilbara bioregion of Western Australia. *Zoolaxa* 3383, 15–38.
- HARVEY M S 1988. A new troglobitic schizomid from Cape Range, Western Australia (Chelicerata: Schizomida). Records of the Western Australian Museum 14, 15–20.
- HARVEY M S 1995a. Barbaraella gen. nov. and Cacoxylus Beier (Pseudoscorpionda: Chernetidae), two remarkable sexually dimorphic pseudoscorpions from Australasia. Records of the Western Australian Museum, Supplement 52, 199–208.
- Harvey M S 1995b. The systematics of the spider family Nicodamidae (Araneae: Amaurobioidea). *Invertebrate Taxonomy* 9, 279–386.
- Harvey M S 1996. Two new species of the water mite genus Penemideopsis from Western Australia (Acarina: Mideopsidae). Records of the Western Australian Museum 17, 443–446.
- HARVEY M S 1998a. The Australian water mites: a guide to the families and genera. CSIRO Publishing, Melbourne.
- HARVEY M S 1998b. Unusual new water mites (Acari: Hydracarina) from Australia, part 1. Records of the Western Australian Museum 19, 91–106.
- HARVEY M S 2001. New cave-dwelling schizomids (Schizomida: Hubbardiidae) from Australia. Records of the Western Australian Museum, Supplement 64, 171–185.
- HARVEY M S 2002. A new species of Austrarchaea (Araneae: Archaeidae) from Western Australia. Records of the Western Australian Museum 21, 35–37.
- Harvey M S 2012. A new species of Synsphyronus (Pseudoscorpiones: Garypidae) from Western Australia. Records of the Western Australian Museum 27, 55-61.
- HARVEY M S, BERRY O, EOWARD K L & HUMPHREYS G 2008. Molecular and morphological systematics of hypogean schizomids (Schizomida: Hubbardiidae) in semi-arid Australia. *Invertebrate Systematics* 22, 167–194.
- HARVEY M S & EDWARD K L 2007. A review of the pseudoscorpion genus *Ideoblothrus* (Pseudoscorpiones, Syarinidae) from western and northern Australia. *Journal of Natural History* 41, 445–472.
- HARVEY M S & HUMPHREYS W F 1995. Notes on the genus Draculoides Harvey (Schizomida: Hubbardiidae), with the description of a new troglobitic species. Records of the Western Australian Museum, Supplement 52, 183–189.
- HARVEY M S & LENG M C 2008. The first troglomorphic pseudoscorpion of the family Olpiidae (Pseudoscorpiones), with remarks on the composition of the family. *Records of the Western Australian Museum* 24, 387–394.

- HARVEY M S, RAHMADI C & ALAND K 2012b. The first record of whip spiders (Amblypygi) in Western Australia. *Australasian Arachnology* 84, 8–9.
- HARVEY M S & VOLSCHENK E S 2007. The systematics of the Gondwanan pseudoscorpion family Hyidae (Pseudoscorpiones: Neobisioidea): new data and a revised phylogenetic hypothesis. *Invertebrate Systematics* 21, 365–406.
- HIRST S 1928. On some Australian species of Trombidiidae. Proceedings of the Zoological Society of London 1928, 1021–1034.
- HODGKIN E P 1995. Barbara York Main. Records of the Western Australian Museum, Supplement 52, vii-xv.
- Hogg H R 1914. Spiders from the Montebello Islands. Proceedings of the Zoological Society of London 1914, 69–92.
- Humphreys W F 1983. The surface of spiders' eggs. Journal of Zoology, London 200, 303–316.
- Humphreys W F 1987. The accoutrements of spiders' eggs (Araneae) with an exploration of their functional importance. Zoological Journal of the Linnean Society 89, 171–201.
- Humphreys W F 1990. The biology of a troglobitic schizomid (Chelicerata: Arachnida) from caves in the semi-arid Cape Range, Western Australia. *Acta Zoologica Fennica* 190, 181–186.
- Humphreys W F 1993. Cave fauna in semi-arid tropical Western Australia: a diverse relict wet-forest litter fauna. *Mémoires de Biospéologie* 20, 105–110.
- Humphreys W F 1995. Chorion surface features of chelicerate eggs. Records of the Western Australian Museum, Supplement 52, 171–181.
- Humphreys W F 2001. The subterranean fauna of Barrow Island, northwestern Australia, and its environment. *Mémoires de Biospéologie* 28, 107–127.
- Humphreys W F, Adams M & Vine B 1989. The biology of *Schizomus vinei* (Chelicerata: Schizomida) in the caves of Cape Range, Western Australia. *Journal of Zoology, Londou* 217, 177–201.
- KEIGHERY G J, HALSE S A, HARVEY M S & MCKENZIE N L 2004. A biodiversity survey of the Western Australian agricultural zone. Records of the Western Australian Museum, Supplement 67
- Koch L E 1963. Nomenclature of an *Urodacus* scorpion from Western Australia. Western Australian Naturalist 9, 22.
- KOCH L E 1970. Predation of the scorpion, Urodacus luplurus, by the lizard, Varanus gouldi. Western Australian Naturalist 11, 120–121.
- Koch L E 1977. The taxonomy, geographic distribution and evolutionary radiation of Australo-Papuan scorpions. *Records of the Western Australian Museum* 5, 83–367.
- Koch L E 1978. A comparative study of the structure, function and adaptation to different habitats of burrows in the scorpion genus *Urodacus* (Scorpionida, Scorpionidae). *Records of the Western Australian Museum* 6, 119–146.
- Koch L E 1981. The scorpions of Australia: aspects of their ecology and zoogeography. *In:* Keast A (ed.) *Ecological biogeography of Australia* 2, pp. 875–884. W Junk, The Hague.
- KOCH L E 1983a. Revision of the Australian centipedes of the genus Cormocephalus Newport (Chilopoda: Scolopendridae: Scolopendrinae). Australian Journal of Zoology 31, 799–833.
- Koch L E 1983b. A taxonomic study of the centipede genus Ethmostigmus Pocock (Chilopoda: Scolopendridae: Otostigminae) in Australia. Australian Journal of Zoology 31, 835–849.
- KOCH L E & COLLESS D H 1986. Numerical taxonomy of Australian species of nine genera of scolopendrid centipedes (Chilopoda: Scolopendridae). Australian Journal of Zoology 34, 87–105.
- Kraepelin K 1908. Scorpiones. *Die Fauna Südwest-Australiens* **2(7)**, 87–104. Gustav Fischer, Jena.
- Kraepelin K 1916. Results Dr E. Mjöberg's Swedish Scientific

- Expeditions Australia 1910–1013. Scolopendriden und skorpione. Arkiv för Zoologi 10, 1–43.
- Krantz G W & Walter D E (Editors) 2009. A manual of acarology (3rd edition). Texas Tech University Press, Lubbock.
- Langlands P, Brennan K & Pearson D 2006. Spiders, spinifex, rainfall and fire: long-term changes in an arid spider assemblage. *Journal of Arid Environments* 67, 36–59.
- Langlands P R, Brennan K E, Framenau V W & Main B Y 2010. Predicting the post-fire responses of animal assemblages: testing a trait-based approach using spiders. *Journal of Animal Ecology* 80, 558–568.
- LOHMANN H 1909. Marine Hydrachnidae und Halacaridae. Fauna Südwest-Australiens 2, 151–154. Gustav Fischer, Jena.
- Main B Y 1952. Notes on the genus *ldiosoma*, a supposedly rare Western Australian trap-door spider. Western Australian Naturalist 3, 130–137.
- MAIN B Y 1957. Biology of aganippine trapdoor spiders (Mygalomorphae: Ctenizidae). Australian Journal of Zoology 5, 402–473.
- Main B Y 1967. Between Wodjil and Tor. Jacaranda Press and Landfall Press, Brisbane.
- MAIN BY 1976. Spiders. Collins, Sydney.
- MAIN BY 1984. Spiders (2nd edition) Collins, Sydney.
- Main B Y 1985. Further studies on the systematics of ctenizid trapdoor spiders: a review of the Australian genera (Araneae: Mygalomorphae: Ctenizidae). *Australian Journal of Zoology, Supplementary Series* 108, 1–84.
- MAIN B Y 1991. Kimberley spiders: rainforest strongholds. *In*: McKenzie N L, Johnston R B & Kendrick P G (eds) *Kimberley Rainforests Australia*, pp. 271–293. Surrey Beatty & Sons, Chipping Norton.
- Main B Y 1993. From flood avoidance to foraging: adaptive shifts in trapdoor spider behaviour. *Memoirs of the Queensland Museum* **33**, 599–606.
- MAIN B Y 1998. Granite outcrops: a collective ecosystem. *Journal of the Royal Society of Western Australia* 80, 113–122.
- MAIN BY 1999. Biological anachronisms among trapdoor spiders reflect Australia's environmental changes since the Mesozoic. *In:* Ponder W & Lunney D (eds) *The other 99%. The conservation and biodiversity of invertebrates*, pp. 236–245. Transactions of the Royal Zoological Society of New South Wales, Mossman.
- MAIN B Y 2001a. Habitat template for invertebrates on granite outcrops. *Journal of the Royal Society of Western Australia* 83, 139–147.
- MAIN B Y 2001b. Historical ecology, responses to current ecological changes and conservation of Australian spiders. *Journal of Insect Conservation* 5, 9–25.
- Main B Y & Framenau V W 2009. A new genus of mygalomorph spider from the Great Victoria Desert and neighbouring arid country in south-eastern Western Australia (Araneae: Nemesiidae). Records of the Western Australian Museum 25, 277–285.
- MAIN B Y & HARVEY M S 1992. Type material of spiders (Chelicerata: Araneae) collected on the Michaelsen and Hartmeyer Expedition of 1905 and lodged in the Western Australian Museum. Records of the Western Australian Museum 15, 703–712.
- MAIN BY, SAMPEY A & WEST P L J 2000. Mygalomorph spiders of the southern Carnarvon Basin, Western Australia. Records of the Western Australian Museum, Supplement 61, 281–293.
- MASON L D, TOMLINSON S, WITHERS P C & MAIN B Y 2013. Thermal and hygric physiology of Australian burrowing mygalomorph spiders (*Aganippe* spp.). *Journal of Comparative Physiology B* 183, 71–82.
- McKay R J 1973. The wolf spiders of Australia (Araneae: Lycosidae): 1. the *bicolor* group. *Memoirs of the Queensland Museum* 16, 375–398.

- McKay R J 1985a. Arachnida: Araneomorphae: Lycosidae. Zoological catalogue of Australia 3, 73–88. Australian Government Publishing Service, Canberra.
- McKay R J 1985b. The wolf spiders of Australia (Araneae: Lycosidae), 14. A new species of the genus *Pardosa*. *Memoirs of the Queensland Museum* 22, 101–105.
- McKenzie N L, Johnston R B & Kendrick P G (Editors) 1991. Kimberley Rainforests Australia, pp. 271–293. Surrey Beatty & Sons, Chipping Norton.
- MICHAELSEN W & HARTMEYER R 1907–1908. Die Fanna Siidwest-Australiens. Gustav Fischer, Jena.
- POCOCK R I 1891. Notes on some scorpions collected by Mr. J.J. Walker, with descriptions of two new species and a new genus. *Annals and Magazine of Natural History* (6)8, 241–247.
- Pocock R I 1898. The Australian scorpions of the genus *Urodacus*, Pet. *Annals and Magazine of Natural History* (7)2, 59–67.
- POCOCK R I 1902. A contribution to the systematics of scorpions. Annals and Magazine of Natural History (7)10, 364–380.
- Prescott J A & Brookes H M 1961. Duncan Campbell Swan, M.Sc. 1907–1960. Transactions of the Royal Society of Sonth Australia 85, 224–225.
- RAINBOW W J 1914. Studies in Australian Araneidae. No. 6. The Terretelariae. Records of the Australian Museum 10, 187–270.
- Rainbow W J & Pulleine R H 1918. Australian trap-door spiders. Records of the Australian Museum 12, 81–169.
- RAVEN R J 1978. Systematics of the spider subfamily Hexathelinae (Dipluridae: Mygalomorphae: Arachnida). Australian Journal of Zoology, Supplementary Series 65, 1–75.
- Rix M G & Harvey M S 2012. Australian assassins, part II: A review of the new assassin spider genus *Zephyrarchaea* (Araneae, Archaeidae) from southern Australia. *Zookeys* 191, 1–62.
- Rix M G, Harvey M S & Roberts J D 2010. A revision of the textricellin spider genus *Raveniella* (Araneae: Araneoidea: Micropholcommatidae): exploring patterns of phylogeny and biogeography in an Australian biodiversity hotspot. *Invertebrate Systematics* 24, 209–237.
- ROEWER C F 1929. Contributions to the fauna of Rottnest Island. No. V. Opiliones in the Western Australian Museum. *Journal of the Royal Society of Western Australia* 15, 95–98.
- Serventy D L 1963. Obituary L. Glauert, M.B.E. Western Australian Naturalist 8, 189–193.

- Simon E 1908. Araneae, 1re partie. *Die Fauna Südwest-Australiens* 1, 359–446. Gustav Fischer, Jena.
- SIMON E 1909. Araneae, 2me partie. Die Fanna Siidwest-Australiens 2, 155–212. Gustav Fischer, Jena.
- SMITH G T 1990. Potential lifetime fecundity and the factors affecting annual fecundity in *Urodacus armatus* (Scorpiones, Scorpionidae). *Journal of Arachnology* 18, 271–280.
- SMITH G T 1998. Density of the burrowing scorpion *Urodacus* armatus in relation to vegetation types: implications for population decline following agricultural clearing. *Pacific Conservation Biology* 4, 209–214.
- SMITH G T & MCKENZIE N L 2000. Biogeography of scorpion communities in the southern Carnarvon Basin, Western Australia. Records of the Western Anstralian Museum, Supplement 61, 269–279.
- Swan D C 1931. On a new species of *Ixodes* (*Ix. hydromyidis*) from Western Australia. *Parasitology* **23**, 485–487.
- Tullgren A 1909. Chelonethi. Die Fanna S\(\textit{n}\)dwest-Australiens 2, 411-415. Gustav Fischer, Jena.
- VINE B, KNOTT B & HUMPHREYS W F 1988. Observations on the environment and biology of *Schizomns vinei* (Chelicerata: Schizomida) from Cape Range, Western Australia. *Records of the Western Australian Museum* 14, 21–34.
- Volschenk E S, Harvey M S & Prendini L 2012. A new species of *Urodacus* (Scorpiones: Urodacidae) from Western Australia. *American Museum Novitates* 3748, 1–18.
- VOLSCHENK E S, SMITH G T & HARVEY M S 2000. A new species of *Urodacus* from Western Australia, with descriptive notes on *Urodacus megamastigus* (Scorpiones: Urodacidae). *Records of the Western Anstralian Musenm* 20, 57–68.
- WALDOCK J M 1995. A new species of Maratus from southwestern Australia (Araneae: Salticidae). Records of the Western Australian Museum, Supplement 52, 165–169.
- WALDOCK J M 2009. A new species of jumping spider of the genus Paraplatoides (Araneae: Salticidae) from Western Australia. Records of the Western Australian Museum 25, 305– 308.
- ŻABKA M & WALDOCK J M 2012. Salticidae (Arachnida: Araneae) from Oriental, Australian and Pacific Regions. Genus Cosmophasis Simon, 1901. Annales Zoologici, Warsaw 62, 115–198.

Received 9 May 2013; accepted 18 December 2013

Relicts, reproduction and reintroductions—a century of marsupial research in Western Australia

N M WARBURTON

School of Veterinary and Life Sciences, Murdoch University, South Street, Murdoch WA 6150, Australia and Department of Earth and Planetary Science, Western Australian Museum, Locked Bag 49, Welshpool DC,WA 6986, Australia N.Warburtou@murdoch.edu.au

Marsupials, the quintessential Australian animals, have attracted considerable interest from the scientific community, both at home and abroad. Nowhere is this more evident than in Western Australia. The following review provides an overview of the history of marsupial research in Western Australia, outlining major contributors and findings along the way. Most research can be grouped within one or more of three major study streams; taxonomy and natural history ('relicts'); reproductive biology and physiology ('reproduction') and conservation ecology ('reintroductions'). Four Australidelphian marsupial orders are represented among the Western Australian fauna: Dasyuromorphia, Peramelemorphia, Diprotodontia and Notoryctemorphia. Many of these species are endemic to Western Australia, some of which represent isolated relicts of ancient phylogenetic lines. Contemporary threatening processes, including habitat change or loss, changes in fire regime and introduced predators, have led to 'modern' relicts, many of which exist in very small, disjointed remnants of their former geographical range. The experimental study of Australian marsupials was pioneered by H 'Harry' Waring, who saw the potential for the application of classical physiological techniques to the unstudied marsupial fauna. The establishment of the field research station at Rottnest Island led to an array of studies of the ecology and physiology of the quokka (Setonix brachyurus) from the 1950s to the early 1970s. These became a platform for our understanding of marsupial reproductive biology. More recently, research on the ecophysiology, genetics and immunology of Western Australian marsupials has been strongly tied to conservation. A major management tool has been to use these studies to guide threatened species translocations and similar conservation attempts.

KEYWORDS: conservation, diversity, Marsupialia, reproductive biology, Western Australia.

INTRODUCTION

Marsupials are recognised throughout the world as the quintessential Australian animals (along with dangerous spiders and venomous snakes). The term marsupial is derived from the Latin 'marsupium', meaning pouch, and is used to encompass a group of mammals (the subclass Marsupialia; formerly Metatheria) that was seen, historically, to have a reproductive system and strategy that was 'intermediate' between the egg-laying Prototheria (monotremes) and the placenta-bearing Eutheria (eutherian or 'placental' mammals). The Gondwanan distribution of extant marsupials was also believed to be reflective of this group having been outcompeted on the other continents by eutherian mammals. Thus, since their earliest encounters with Europeans, marsupials were regarded as the 'poor cousins' of the evolutionarily 'superior' eutherian mammals. Research in Western Australia during the last century has, however, helped to dramatically change this view. Marsupialia is now recognised as the evolutionary sister group to the Eutheria. That research has also provided some fascinating insight into the ecology and evolution of the 'pouched mammals'.

RELICTS

While the 'flying' kangaroo and koala 'bears' are easily recognised, the diversity of marsupial fauna is less

widely known. Among the marsupials of Australia and New Guinea (the Australidelphian radiation of marsupials) there are four recognised groups: carnivorous marsupials (Order: Dasyuromorphia); omnivorous bandicoots and bilbies (Peramelemorphia); principally herbivorous possums, wombats, koalas, kangaroos and their kin (Diprotodontia); and fossorial marsupial moles (Notoryctemorphia). All four Australidelphian marsupial orders are represented among the Western Australian fauna (Appendix 1). In his presidential address of 1948 to the Royal Society of Western Australia, Glauert (1950) presented a historical account of the early descriptions and development of knowledge of the marsupials of Western Australia. There are numerous species endemic to Western Australia, some of which represent isolated relicts of ancient phylogenetic lines as a consequence of divergent evolution (e.g. bilbies Macrotis lagotis and numbats Myrmecobius fasciatus: Archer & Kirsch 1977) and others following past extinction events (i.e. megafaunal extinctions in which 90% of Australia's large mammals went extinct during the Pleistocene: Merrilees 1968; Prideaux et al. 2007b).

The last century has also seen a massive decline in the number, diversity and distribution of marsupials in Australia, nowhere more so than in the west. These contemporary threatening processes have led to 'modern' relicts, many of which exist in very small, disjointed remnants of their former geographical range. Numerous studies have highlighted the key threatening processes in this decline, including diversion/reduction in

resources, vegetation changes in response to exotic herbivores and dieback disease, changes in fire regime, and introduced predators (e.g. foxes and cats) (Archer 1974; Jenkins 1974; Calver & Dell 1999; Fletcher & Morris 2003; Friend & Wayne 2003; de Tores *et al.* 2007). Burbidge & McKenzie (1989) coined the term 'critical weight range' (CWR) to define the marsupial species most susceptible to these threats: medium-sized (35–5500 g), terrestrial animals of the semiarid and arid zones (Johnson & Isaac 2009). Yet, at a time when the extinction of more marsupial species is a real possibility, we are still discovering the true diversity and evolutionary history of Western Australian marsupials.

Dasyuromorphia comprises three families: Dasyuridae (dasyurids), the monotypic Myrmecobiidae (numbat), and Thylacinidae (thyacine). Western Australia is home to a large diversity of small to very small, arid adapted dasyurids, especially dunnarts (*Sminthopsis* spp.; Figure 1a) which typically range in body mass between 10 and 40 g, but also *Pseudantechinus* spp. (15–50 g), the kaluta (*Dasykaluta rosamondae*; 25–40 g), *Ningaui* spp. (6.5–10.5 g: Figure 1b) and *Planigale* spp. (4–10 g). In contrast, mesic genera such as *Antechinus* and the larger bodied *Dasyurus* are represented by only a few species in Western Australia (e.g. the mardo, *Antechinus flavipes*; and northern and western quolls, *Dasyurus hallucatus* and *D*.

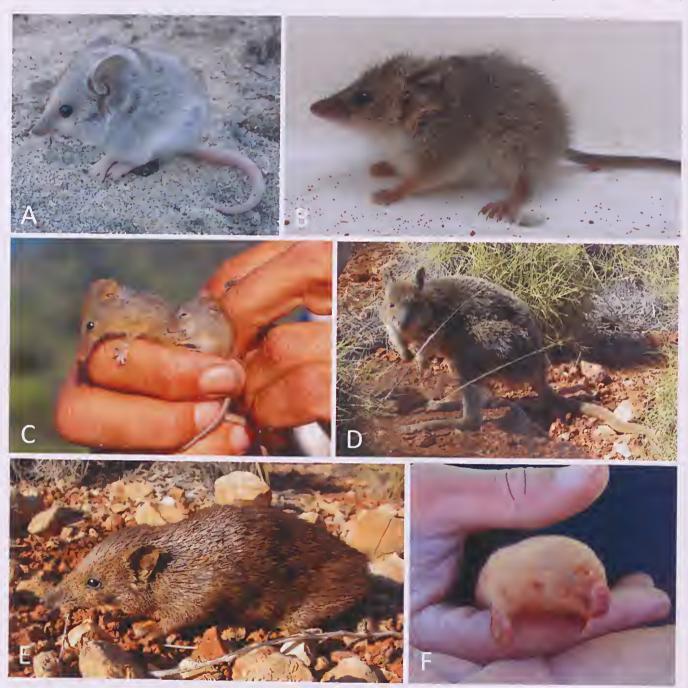


Figure 1 Representative marsupials of Western Australia. (a) White-tailed dunnart, Sminthopsis granulipes. (b) Wongai ningaui, Ningaui ridei. (c) Honey possum, Tarsipes rostratus. (d) Spectacled hare-wallaby, Lagorchestes conspicillatus conspicillatus. (e) Golden bandicoot, Isoodon auratus barrowensis. (f) Northern marsupial mole, Notoryctes caurinus. (a–e) courtesy of W Bancroft; (f) courtesy of I Harris.

geoffroii). Endemic CWR species in the mid-west and southwest such as the dibbler (Parantechinus apicalis), redtailed phascogale (Phascogale calura) and the numbat have suffered enormously from habitat fragmentation and predation by introduced foxes and cats; and are now restricted to tiny pockets of their original distribution (Woolley 1977, 1980; Morcombe 1967; Burbidge & McKenzie 1989). The numbat is unusual among marsupials in being diurnal and feeding exclusively on termites. It has long been recognised as distinct from other dasyurids on the basis of dental morphology, and basicranial skull structure suggested that Myrmecobiidae was an early divergence from the dasyuroid line (Archer & Kirsch 1977). The now extinct thylacine, however, represented the youngest form of a previously much more diverse family (Murray & Megirian, 2000), distinct from other marsupial carnivores (Archer 1976).

Bandicoots (family Peramelidae) are medium-sized, terrestrial, omnivorous marsupials with a bounding gait and forelimbs adapted for digging for food (Gordon & Hulbert 1989). Approximately 20 species of bandicoots are known from Australia and New Guinea, eight of which have distributions (at least historically) that include Western Australia. While Western Australian populations of tropical northern brown bandicoot (Isoodon macrourus) and mesic southern brown bandicoots (Isoodou obesulus) are stable (IUCN 2012), only small remnant populations remain of western barred bandicoots (Perameles bougainville, on the islands of Shark Bay) and golden bandicoot (I. auratus barroweusis, in the Kimberley and islands off the northwest coast: Figure 1e). Bilbies (Macrotis lagotis; Thylacomyidae), aridadapted allies of the bandicoots, persist in scattered colonies in the Pilbara and Kimberley (Troughton 1932; Jenkins 1974; Friend et al. 2008b), while the lesser bilby (M. leucura) and pig-footed bandicoot (Chaeropus ecaudatus; Chaeropodidae) have become extinct during the twentieth century (Burbidge et al. 2008a, c). While bilbies have had significant publicity, most bandicoots are unremarkable in appearance; and though the southern brown bandicoot is often encountered in gardens in the southwest, little recognition is given to how interesting these marsupials are. The bandicoot skeleton has an unusual combination of a plesiomorphic polyprotodont dentition with derived syndactylous hindlimbs, in which the second and third digits of the foot are relatively reduced in size and bound together developmentally. Bandicoots also have an ossified patella, uncommon among marsupials, and lack a clavicle within the pectoral girdle. The syndactylous pes was historically thought to reflect a close evolutionary relationship with diprotodonts; however, craniodental morphology (Archer 1976) and molecular studies (Springer et al. 1998) refuted this view, and suggested a much more ancient origin for the bandicoot group. The reproductive strategy of bandicoots has been of great interest. Bandicoots have among the shortest gestation of any mammals, as short as 12.5 days, and may produce a litter every 60 days in favourable conditions. This great efficiency in reproduction is accomplished by the development of a relatively (among marsupials) complex allantoic placenta and production of very rich milk (Tyndale-Biscoe 2005).

Diprotodonts are principally arboreal herbivores and

consequently are less diverse in Western Australia than in the more heavily forested areas of eastern Australia. The handful of Western Australian species include the scaly-tailed possum (Wyulda squamicaudata) endemic to rocky outcrops of the Kimberley region (Alexander 1918; Calaby 1957; Runcie 1999); the ubiquitous brush tail possum (Trichosurus vulpecula), the western ringtail possum (Pseudocheirus occidentalis) found in localised forest patches of the coastal South West (especially peppermint trees threatened by coastal development) (Wright et al. 2007; Thompson & Thompson 2009), the tropical rock ringtail possum (Petropseudes dahli) and the western pygmy possum (Cercartetus conciunus) of southern Australia. The most intensively studied is the honey possum, Tarsipes rostratus (monotypic Family Tarsipedidae: Figure 1c), which feeds exclusively on nectar and pollen (Glauert 1929; Vose 1973; Wiens et al. 1980) and displays a suite of adaptations to this unusual diet (Parker 1890; Richardson et al. 1986; Slaven & Richardson 1988; Bradshaw & Bradshaw 2012). The honey possum was used to demonstrate the potential for trichromatic vision in marsupials and has adaptations of the visual system for the detection of mature Bauksia attenuata flowers, their favoured food source (Arrese et al. 2002; Sumner et al. 2005; Cowing et al. 2008). This tiny marsupial (males 7-9 g; females 10-12 g) also has the distinction of having both the largest testes relative to body mass (4.2%) and the longest sperm among mammals (up to 360 µm) (Wooller et al. 1981; Renfree et al. 1984).

Kangaroos and related taxa (superfamily Macropodoidea) represent the largest terrestrial radiation of the Diprotodontia. Macropodoids of medium to large body size (>10 kg) especially those of the genus Macropus are relatively common and often have broad distributions (IUCN 2012): western grey kangaroo (M. fuligiuosus) and western brush wallaby (M. irma) in the south; red kangaroo (M. rufus) and euro (M. robustus) through the semiarid and arid country; and the agile wallaby (M. agilis), antilopine wallaroo (M. autilopiuus) and northern nailtail wallaby (Onychogalea unguifera) in the tropical north. A divergent array of rock-wallaby species is also found in Western Australia including the monjon (Petrogale burbidgei), the smallest of the rock-wallabies (Kitchener & Sanson 1978), and the narbarlek (P. coucinua), which, uniquely among marsupials, has the potential to develop unlimited numbers of supernumary molar teeth (Sanson et al. 1985). W D L Ride, Director of the Western Australian Museum (1957-1975) contributed significantly to our understanding of the evolution of macropodoids (Ride 1957, 1959, 1961, 1962, 1971a, b, 1979; Ride & Serventy 1963).

Small- to medium-sized macropodoids have suffered heavily through loss of habitat and predation or competition by ferals and domestics. Those that have managed to persist are found in small remnants of their former distribution. The burrowing bettong (Bettongia lesueur) and rufous hare-wallaby (Lagorchestes hirsutus) are now restricted to populations on Barrow Island and the islands of Shark Bay, and the spectacled hare-wallaby (L. conspicillatus: Figure 1d) is reduced in range, while Gilbert's potoroo (Potorous gilbertii) on the south coast is among the most critically endangered of all mammals (Sinclair et al. 2002). The tammar wallaby (M. eugenii)

and quokka remain in isolated mainland and island populations in the south west (Main 1961; Eldridge et al. 2004; de Tores et al. 2007) and explanations as to recent crashes of the formerly recovered populations of the woylie (Bettongia penicillata) have proven elusive (Groom 2010; Pacioni et al. 2011; Rong et al. 2012). The banded hare-wallaby (Lagostrophus fasciatus), extinct on the mainland and found only on Bernier and Dorre Islands in Shark Bay, provides an interesting case study on the evolution of macropodoid marsupials. It has many unusual features of craniodental (Flannery 1983; Prideaux 2004), musculoskeletal (Warburton 2009) and reproductive anatomy (Tyndale-Biscoe 1965) which have made it difficult to place within the kangaroo family tree (Flannery 1983; Westerman et al. 2002; Nilsson 2006). Previously hypothesised as the sole survivor of the otherwise extinct group of giant, short-faced sthenurine kangaroos, it has most recently been proposed to be the living relic of a more ancient phylogenetic line, subfamily Lagostrophinae (Prideaux & Warburton 2010).

Marsupial moles are highly specialised burrowing marsupials adapted to life underground. These small marsupials (30–70 g) lack eyes and external ears and possess short, stout limbs that are highly modified for digging. Two species are recognised: the central marsupial mole (*Notoryctes typhlops*) and the northern marsupial mole (*N. caurinus*: Figure 1f), the latter endemic to the Pilbara region of Western Australia (Thomas 1920; Corbett 1975; Benshemesh & Johnson 2003). Relatively little is known about these cryptic marsupials, and apart from morphological (Warburton 2006) and physiological (Withers *et al.* 2000) work based on opportunistic specimen finds, few recent studies have been undertaken.

In addition to the extant species, there is a rich, albeit relatively recent, fossil history of marsupials in Western Australia that has attracted the interest of a number of researchers including Royal Society Western Australia past presidents L Glauert (1933-1934, 1947-1949), W D L Ride (1962–1963) and D Merrilees (1966–1967). Principally late Pleistocene in age (126–12 ka) the caves of the Margaret River region (Mammoth Cave, Devil's Lair, Kudjal Yolgah Cave and Tight Entrance Cave) have yielded fossils of a number of extinct marsupials including the marsupial 'lion' (Thylacoleo carnifex), wombats, the large diprotodontid Zygomaturus, and giant sthenurine (short-faced) kangaroos (Glauert 1910, 1912, 1914, 1921, 1926, 1948; Merrilees 1965, 1967, 1970a, b; Archer & Baynes 1972). Additionally these caves have yielded evidence of the interaction of Aboriginal people with some of these animals (Archer et al. 1980). Caves in the Nullarbor region range from early Pleistocene (2.6 Ma-781 ka) to Holocene (<12 ka) and have provided unprecedented opportunities to study the diversity and ecology of extinct species due to the exquisite preservation of semi-articulated specimens (Lundelius 1963; Lowry & Lowry 1967; Lowry & Merrilees 1969; Lundelius & Turnbull 1973, 1981; Prideaux et al. 2007a). Among these deposits are a large diversity of marsupials, including many species of kangaroos including treekangaroos (Prideaux et al. 2007a; Prideaux & Warburton 2008, 2009). The fossil deposits in Western Australia have been key to current understanding of the timing of Pleistocene extinctions of the Australian megafauna and

the factors (interactions of climate/hunting/fire) leading to the drastic changes in biodiversity during this period (Merrilees 1968; Roberts *et al.* 2001; Prideaux *et al.* 2007b; Prideaux *et al.* 2009).

ECOLOGY, PHYSIOLOGY AND REPRODUCTION

Ecology and general physiology

The experimental study of Australian marsupials was pioneered by H 'Harry' Waring, Professor of Zoology at the University of Western Australia 1948–1975, who saw the potential for the application of classical physiological techniques to the unstudied marsupial fauna (Waring 1959). Waring sought and achieved the establishment of a field research station on Rottnest Island (off the Perth coast) and, together with graduate students and colleagues, produced significant early advances in marsupial physiology using the quokka as a model. These studies fell into two main areas, physiological ecology and reproductive physiology, and paved the way for the current understanding of marsupial biology and reproduction.

Ecological studies examined aspects of breeding and growth of pouch young (Shield & Woolley 1963; Shield 1964, 1968), population studies (Dunnet 1962, 1963; Shield & Woolley 1963), and habitat use (Storr 1964; Nicholls 1971; Kitchener 1972, 1973). An experimental approach was taken up to investigate aspects of marsupial physiology, including digestive physiology (Moir et al. 1954; Waring et al. 1966), thermoregulation (Bartholomew 1956; Kinnear & Shield 1975), and osmoregulation (Bentley 1955; Barker & Barker 1959; Bentley & Shield 1962; Bakker & Main 1980). These studies on the quokka became a platform for our understanding of marsupial physiology. Conscious of a single-species approach, however, Main (1983) examined the extent to which studies on the quokka could be extrapolated to marsupials more generally. His review drew together the quokka research with studies of other macropods, to assimilate aspects of ecophysiology of macropods, as well as to broader theoretical principles. Many of the results and interpretations from the study of the quokka were shown to be more widely testable and applicable for macropod marsupials. Studies of marsupial ecophysiology, or how an animal 'works' in its environment, have become an important tool in the conservation and management of threatened species.

The highly specialised diet and/or behaviour of some marsupials in relation to their diet have been of particular interest for physiological studies, and Western Australia has provided numerous oddities in this regard. For example, tammars on the Abrolhos Islands are able to drink seawater and maintain body weight while eating poor-quality dry graze (Kinnear et al. 1968). Tammars survive this extreme water and nutrient deficit by a combination of marsupial characteristics and physiological adaptations. All marsupials have a relatively low basal metabolic rate (BMR) and a depressed nitrogen metabolism in comparison to eutherian mammals, resulting in a relatively lower requirement for these nutrients generally (Fraser & Kinnear 1969). But tammars are also able to recycle urea

nitrogen throughout the dry season, by cyclic exchange of nitrogen between their body tissues and the microbial community within the pregastric (forestomach) portion of the digestive system, further reducing their nitrogen requirements (Kinnear & Main 1975). In order to cope with the salt loading resulting from drinking saltwater, tammar kidneys have been shown to concentrate urinary electrolytes to a greater degree than highly specialised eutherian mammals (Kinnear et al. 1968).

The physiological variables most commonly used to make inferences about the relationship of an animal to its environment are body temperature and metabolic rate (a measure of the total energy used by an animal per unit time). This has been a dominant theme of Western Australian research over many decades (Kinnear & Shield 1975; Withers et al. 2000, 2006). As a general rule, marsupials have a lower body temperature and metabolic rate than eutherian mammals of equivalent size (Hume 1999) which, as with the marsupial reproductive strategy, has been hypothesised to be a result of the relatively low productivity of the Australian environment (Tyndale-Biscoe 2001). One particular physiological characteristic of a number of marsupials is an ability to enter shallow, daily torpor to reduce energy use when food resources are scarce or during adverse environmental conditions. Torpor is indicated physiologically by a significant drop in BMR and body temperature. A number of Western Australian marsupials enter torpor in order to conserve energy, including the honey possum (Withers et al. 1990), numbats (Cooper & Withers 2004) and many dasyurids (Geiser 1994). Cooper & Geiser (2008) reviewed the relationship between body mass, BMR and thermoregulation and demonstrated that shallow, shortterm (daily) torpor is an adaptive physiological mechanism, rather than an inability to maintain body temperature. Investigations of neural control of the heart in the fat-tailed dunnart (Zosky & O'Shea 2003) and western pygmy possum (Zosky & Larcombe 2003) found that torpor is regulated by a physiological decrease in heart rate, under the control of the autonomic nervous system. This mechanism is homogeneous with that found in deep ('true') hibernators, such as bats, suggesting a greater overall similarity between shallow torpor and deep hibernation than was previously recognised.

Two other fields of marsupial physiology have seen significant advancement in Western Australia: immunology (the physiological functioning of the immune system) and endocrinology (the study of hormones, their functions and the glands or tissues that secrete them). Again, the quokka was the subject for much of the early work (Bradshaw 1983a; Stanley 1983). The development of the immune system was of considerable interest, given the altricial nature of marsupials at birth. Two immunological mechanisms were found to help protect marsupial neonates in their relatively underdeveloped state. Initially there is a passive transfer of maternal antibodies to the pouch young through the milk (Yadav 1971). However, the digestive tract is only able to absorb antibodies during pouch life and only a proportion of antibodies are able to be transferred in this way. Secondly, there is a relatively rapid maturation of immune competence, as evidenced in particular by the early presence of immune cells such as lymphocytes, and a rapid development and functionality of the thymus gland (Stanley et al. 1972; Yadav et al. 1972; Ashman et al. 1975).

Reproduction

Marsupials are distinguished from eutherian ('placental') mammals primarily on the basis of reproductive biology. Marsupial neonates (newborns) are highly altricial at birth; that is they are born in an undeveloped state and, thus, require extensive parental care. Most of the development of the young takes place in the pouch, where the joey is provided with milk by the mother for an extended period of time. All marsupials have fully functioning placentae; they are merely short-lived when compared to those of eutherians (Hill 1900; Flynn 1923; McCrady 1938; Enders & Enders 1969). Eutherian mammals, in comparison, tend to give birth to welldeveloped (precocial) young, though the range in development is significant if one compares a newborn mouse with a newborn calf, which can walk within hours. Reproductive anatomy also differs between marsupials and eutherian mammals. The female reproductive tract of marsupials has two lateral vaginae which each pass to a separate oviduct (uterine tube), rather than two oviducts converging to one uterus, as in most eutherians. The lateral vaginae function as passages for sperm, while an additional median- or pseudo-vagina forms for the passage of young; in most groups the median vagina must be re-formed each breeding season, though in macropods it remains open post-partum (Tyndale-Biscoe 2005). In male marsupials, the testes and scrotum lie anterior to (in front of) the penis, rather than posterior (behind) as in eutherian mammals. The development of other sexual characteristics, such as mammary tissue, nipples and pouch in marsupials has a different genetic signal to that of eutherian mammals, attributed to a different configuration of the sex chromosomes in marsupials; male marsupials do not possess nipples or a pouch (Tyndale-Biscoe 2005). Other differences in anatomy and physiology are apparent throughout the body of marsupials, although those of the reproductive system are perhaps the most obvious.

While gestation in marsupials is short, the lactation period is long in comparison to eutherian mammals of equivalent size (Tyndale-Biscoe 2001). This has been interpreted as a strategy to cope with the relatively low productivity or unpredictable availability of resources within the Australian environment, where the total resource requirements for growth are spread over the extended period of lactation (Tyndale-Biscoe 2001). Other aspects of marsupial reproductive biology have similarly been linked to resource availability. Some marsupials demonstrate embryonic diapause, first described by Sharman (1955b) in the quokka, in which the implantation and development of the embryo is suspended until such time as the mother is capable of supporting the developing embryo. While not unique to marsupials, this adaptive strategy is found in a number of Western Australian species including the honey possum and many macropods (Sadleir & Tyndale-Biscoe 1977; Renfree 1980; Tyndale-Biscoe & Hinds 1981). A more extreme strategy linked to resource availability is male die-off (semelparity; breeding only once in a lifetime), whereby adult males die after breeding; this strategy has the potential to increase juvenile

survivorship by reducing competition for food. Male dieoff has been observed in many Western Australian dasyurids, the largest being the northern quoll (Woolley 1991, 2008e; Crowther 2008; Oakwood 2008; Soderquist & Rhind 2008). In many species this die-off is obligate (i.e. all breeding males die, regardless of resource availability) as a physiological-stress-related response to breeding (Woolley 2008c), while in dibblers and northern quolls it appears to be facultative, and dependent on resource supply (Mills & Bencini 2000; Bradley 2003).

Endocrinology became a key tool for the developing understanding of marsupial biology, particularly with regard to the reproductive cycle of marsupials and the hormonal control of pregnancy (Tyndale-Biscoe et al. 1974; Tyndale-Biscoe 1978; Cake et al. 1980; Tyndale-Biscoe & Hinds 1981). The early studies of the reproductive biology of quokkas (Sharman 1955a, b; Waring et al. 1955) led to Western Australia becoming a centre for the study of reproductive endocrinology. The drive to measure hormonal changes during reproduction in marsupials came from Sharman's (1970) claim that marsupials, unlike eutherians, did not show 'maternal recognition of pregnancy', in other words, that the presence of the embryo in the uterus did not bring about any changes in the physiology of the mother. Because gestation is always contained within a single oestrous cycle in marsupials, and thus pregnancy does not inhibit ovulation, the assumption was made that the hormonal changes throughout an oestrous cycle were all that were need to sustain a pregnancy. This catalysed the development of a specific radioimmunoassay for the hormone progesterone, one of key hormones responsible for the regulation of the female reproductive cycle and pregnancy, to monitor changes throughout both pregnant and non-pregnant cycles. The publication in 1980 of a paper showing the presence of a small but significant spike in progesterone early in the pregnant cycle of the quokka (Cake et al. 1980) unleashed a torrent of criticism from others in the field and led to the initiation of a series of studies in the tammar wallaby (Hinds & Tyndale-Biscoe 1982), and other species of macropods, all of which showed the presence of a similar spike in the pregnant cycle. Hugh Tyndale-Biscoe later described this as one of the most important discoveries in marsupial reproductive physiology of the last few decades (Tyndale-Biscoe 1997).

During the reproductive cycle, progesterone is produced in the ovaries (by the corpus luteum; the remains of the follicle after ovulation) and has a number of roles including preparing the endometrium (the lining of the uterus), and helping to support the implantation of the foetus. The role of the foetus in the process of birth had earlier been indicated by cross-breeding experiments with grey-kangaroos (Poole 1973) and from the shortening of the life-span of the corpus luteum by the foetus in the tammar (Merchant 1979). With the demonstration in both the quokka and the tammar that the placenta is an endocrine organ and capable of secreting progesterone (Heller 1973; Bradshaw et al. 1978; Heap et al. 1980), the marsupial foeto-placental unit was suspected of being more than just a passive occupant of the oestrus cycle. It required the advent of improvement in hormone assays to elaborate the nature of the foetoplacental effect on the mother and the development of

receptor assays for progesterone in uterine tissue (Owen et al. 1982). Importantly, the marsupial foetal adrenal gland was shown to secrete cortisol just prior to birth (Sorokin 1981), and to initiate parturition in the marsupial (Shaw et al. 1996) as is the case in eutherian mammals, in which cortisol is the trigger for the cascade of hormonal events leading to birth. Progesterone profiles throughout pregnancy in the quokka and the tammar also revealed that the foeto-placental unit shortened the life span of the corpus luteum. This was indeed a startling discovery; it is in direct contrast to gestation in most eutheria, in which the foeto-placental unit significantly prolongs the life-span of the corpus luteum (Bradshaw & Bradshaw 2011).

During pregnancy, the placenta also produces progesterone, and the amount of progesterone within the system has an effect of the rate of embryonic development, and the initiation of parturition (birth) and lactation (Bradshaw & Bradshaw 2011). Bradshaw & Bradshaw (2011) reviewed the role of progesterone in marsupials, in comparison with eutherian mammals. In contrast to historical views, these authors highlighted the fact that all of the basic physiological mechanisms of progesterone observed in the extended gestation of eutherian mammals are also measurable in the relatively short gestation of marsupials. Further, measurable effects of progesterone (prior to formation of the corpus luteum) on the induction of sexual behaviour, female receptivity and ovulation in marsupials were noted.

Endocrinology has also provided insight into the control mechanisms of other aspects of marsupial reproductive biology including embryonic diapause. Diapause in macropods is associated with low levels of circulating progesterone and an undeveloped corpus luteum (Tyndale-Biscoe & Hinds 1981). While seasonal photoperiod provides the ultimate control for obligate diapause (embryos fertilised in late autumn remain in a state of diapause until after the summer solstice (Renfree & Shaw 2000), facultative diapause is more flexible. In many species, females mate soon after giving birth and the resulting newly fertilised embryo will remain in a state of diapause while there is a young in the pouch. If the pouch young does not survive, for whatever reason, the absence of suckling triggers activation of the corpus luteum and reactivation of the embryo (Tyndale-Biscoe 1978). Embryonic diapause in honey possums, similarly, has hormonal controls that respond to lactational cues and photoperiod, as well as exhibiting their own entrained rhythm (Oates et al. 2007). To study hormone levels in such tiny, and fragile animals, new methods for examining the hormones present in faeces have been established (Bradshaw et al. 2004; Oates et al. 2004). Such studies have provided significant advances detailing the reproductive physiology of the honey possum (Oates et al. 2007) as well as providing important data for conservation programs including captive breeding programs (Stead-Richardson et al. 2010) and translocation attempts (Mills et al. 2012).

REINTRODUCTION

By the middle of the twentieth century it was recognised that iconic Western Australian species such as the numbat were threatened and that conservation efforts were needed (Fleay 1952; Calaby 1960; Serventy 1962). As noted in preceding sections, the threatening processes are many and varied, and include habitat loss, feral cats, foxes, cane toads, agriculture, fire regimes, logging and climate change. Attempts to conserve species may involve the mitigation or minimisation threats, but where populations are extremely vulnerable this may not be enough. A major management tool has been translocation (movement by humans) of individuals of threatened species to areas from where they were once known but no longer occur (reintroduction) or to areas outside this range but that are considered suitable and secure habitats, for example offshore islands (introduction). It is important to note that, for many species, reliable estimates of population size are not available, and a recently published study on the decline in woylie numbers, by Wayne et al. (2013), highlights the conservation and management implications of 'getting the numbers right'.

The success of a number of translocation attempts of endangered macropodoids was reviewed by Short et al. (1992), including quokka and tammar wallaby to Jandakot between 1971 and 1988, banded hare-wallaby to Dirk Hartog Island in 1974 and woylie to Perup (1977), Collie and Nannup (1982–1983). The majority of these reintroductions was unsuccessful. Mainland populations were under most threat from foxes and cats, though habitat degradation and infection may also have been contributing factors (Short et al. 1992). Reintroductions on islands were significantly more successful than attempts on the mainland. Banded hare-wallabies, however, did not manage to establish a viable population on Dirk Hartog Island. Though Dirk Hartog Island was fox free, it was a pastoral station carrying sheep, with degraded habitat, and large numbers of feral goats and cats (Short et al. 1992). Other documented reintroductions have included burrowing bettong, rufous hare-wallaby, banded hare wallaby and western barred bandicoot as part of the 'Return to Dryandra Project' (Anon. 2012), rufous hare-wallaby and banded hare wallaby to Peron Peninsula (2001) (Hardman & Moro 2006) and numbats into the Arid Recovery Reserve, Roxby Downs, South Australia in 2005 (Bester & Rusten 2009). Often, however, the results of these reintroductions are difficult to monitor, and detailed studies of survivorship over the long-term are not always possible due to lack of funding.

A high profile case study of a successful translocation attempt is that of the critically endangered Gilbert's potoroo, the most endangered mammal in Australia. Gilbert's potoroo was rediscovered in 1994 at Two Peoples Bay reserve near Albany, having been considered extinct for over one hundred years. Fewer than 50 individuals remained and a management programme was established in order to conserve the population by habitat preservation, predator control and captive breeding (Courtenay & Friend 2004). Genetic studies of the population indicated a substantial genetic bottleneck consistent with significant population decline (Sinclair et al. 2002). Captive-breeding attempts have been unsuccessful and faecal hormonal measurements demonstrated a lack of reproductive hormonal activity in captive females (Stead-Richardson et al. 2010). In order to protect the extant population from stochastic events such as fire, and with no sites within the species' former mainland range deemed suitable, 10 animals from the wild population were introduced to Bald Island, a predator-free island off Cheynes Beach, in 2005–2007 (Anon. 2010). The introduction has been successful and a breeding population has established on the island. Following the success at Bald Island, Gilbert's potoroos have been subsequently reintroduced to a mainland site at Waychinicup National Park near Mt Manypeaks (Anon. 2011).

Where translocation is not practicable, the in situ management of persisting populations of threatened species (and the threats) can also be an effective conservation strategy. Almost invariably, predation by introduced foxes and cats is one of the most significant pressures threatening the survival of native species (Kinnear et al. 1988; Hayward et al. 2003; Clarke et al. 2008; Wayne et al. 2011). In some case, the removal of introduced predators has led to the successful management of threatened native species. At the time of European settlement, quokkas were widespread throughout the South West, and their subsequent and critical decline on the mainland was strongly correlated with the arrival of the red fox (Vulpes vulpes) (White 1952; Hayward et al. 2003). In 2003 Hayward et al. found that three of seven previously recorded mainland populations had become extinct, and that those remaining were under serious threat of extinction. In addition to ongoing pressure from predation and habitat changes, the large separation of these populations as a result of habitat fragmentation was a contributing factor to local extinctions. On the basis of metapopulation theory, however, they predicted that appropriate management of local populations through fox control and the restoration of habitat may result in increased population size (Hayward et al. 2003). Seasonal trapping during 2010-2011 demonstrated substantial increases in population size correlated with fox baiting. Viable quokka populations were found at six mainland sites, including two previously pronounced locally extinct (Dundas et al. 2012). Fox baiting has been successful in the management of a number of threatened marsupial species, including the numbat and rock wallabies (Kinnear et al. 1988; de Tores et al. 2007; Wayne et al. 2011). Cats, however, are notoriously difficult to control in open systems (Risbey et al. 1997; Short & Turner 2005).

Obviously, translocations also require in situ management, and a combination of the above approaches can improve success. In practice this requires clear objectives to be set and a commitment to long-term management (Short et al. 1992). An example of the successful outcome of well-thought out and wellmanaged reintroduction programs is that of the dibbler. The dibbler had been considered extinct for almost a century before being rediscovered near the south coast in 1967 (Morcombe 1967). It is currently regarded as endangered (Friend et al. 2008a). A very successful captive breeding program was established at Perth Zoo in 1997 from a colony of wild caught individuals from Whitlock and Boullanger Islands near Jurien Bay. These animals provided study specimens for intensive research into the reproductive biology and behaviour of the dibbler (Lambert & Mills 2006). Subsequently, more than 80 captive bred individuals were released on Escape Island (Jurien Bay) from 1998 to 2000. Radiotelemetry and intensive trapping were used to monitor the Escape Island population. Breeding and dispersal of young were recorded within the first year and by 2001 a third generation of wild-born dibblers had been recruited into the population (Moro 2003). The success of this project reflects the combination of detailed reproductive and ecophysiological research, a clear set of objectives and careful monitoring of reintroduced population.

The success of reintroductions is improved with greater knowledge of species and their ecology to guide conservation attempts. While this is a very broad area of research, many such studies in Western Australia appear to fall into three discrete fields: ecophysiology, genetics and immunology.

That ecophysiological principles could be applied to conservation and management strategies was advocated by Bert Main (Main 1961, 1968; Main & Yadav 1971). Through his series of papers, intensive ecological studies were made of eight macropodoid species on Western Australian offshore islands in order to determine the characteristics of both animals (habitat cover, nutritional and water requirements) and the islands (size, floral diversity including trees) which accounted for the observed diversity of fauna. Following this, he considered the likely implications for the management and conservation of those systems. Main & Yadav (1971) highlighted the importance of Barrow Island as a refuge for many species as a result not only of its large size, but more importantly by the fact that Barrow Island retains the topographic diversity (including stable rocky outcrops) and floral assemblages of the adjacent mainland. In a few instances habitat disturbance has had the opposite effect, for example significant population growth of spectacled hare-wallabies on Barrow Island and quokka on Rottnest Island. In such cases, careful management is required in order to minimise the possible detrimental effects of large population size, especially on islands (Bradshaw 1983b; Bakker & Bradshaw 1989).

More recently, the application of genetic methods and techniques to conservation problems has become an important area of research. Population genetics, as a field, measures genetic variation within and between populations in order to understand patterns of gene flow and evolution of species. It is understood that decreased genetic variation within a population leads to reduced fitness in an evolutionary sense. Conservation genetics, then, seeks to understand genetic variation within populations in order to conserve genetic diversity. Further, it is important to establish baseline data of genetic variation within and between donor and recipient population prior to mixing populations (Alacs et al. 2011). For example, in order to better understand the effects of range reduction on gene flow and genetic variation in the numbat, Fumagalli et al. (1999) analysed mitochondrial DNA (mtDNA) sequences of free-ranging individuals and museum specimens. Though reduced genetic diversity following population decline was evident, relatively recent connectivity between remnant populations was indicated. For management purposes, then, remnant populations could be treated as a single historical lineage and translocation might be a successful strategy for the maintenance of genetic diversity (Fumagalli et al. 1999). Historical patterns of interconnectedness have also been elucidated between

populations of woylie, though genetic variation between populations was evident (Pacioni et al. 2011). In contrast, the genetic diversity of the quokka (measured by microsatellites and other molecular techniques) indicated significant genetic differences between island and mainland populations (Alacs et al. 2011), highlighting the need for caution when considering the translocation of possibly maladapted island individuals to supplement mainland populations of this species; while the Barrow Island population of black-footed rock wallabies has been shown to have the lowest level of genetic variation found in any mammal (Eldridge et al. 1999).

An opportunity to investigate a population response in the face of a threatening process, from a conservation genetics perspective, has been taken up in the case of the northern quoll. Using a variety of genetic markers, How et al. (2009) have investigated the population structure of the northern quoll, which is threatened by the spread of the introduced cane toad (*Chaunus marinus*). Varied patterns of gene-flow between island and mainland populations, and genetic divergence between populations in the Pilbara, Kimberley and offshore islands has implications for conservation of genetic diversity in this keystone marsupial predator (How et al. 2009).

The last two decades have seen a rapid increase in the immunological study of marsupials. Immunological threats to marsupial populations, and particularly captive-bred populations, have led to extensive characterisation of viruses, microbes and parasites in marsupials. Haematological studies may be performed for assessments of animal health as an element of management strategies (Bennett et al. 2007). Such a study in the quokka found differences in the blood characteristics of wild versus captive populations, potentially reflecting nutritional deficiency in the wild. The same study also identified a number of haemoparasites in wild populations of quokka, highlighting the need for more work in order to understand the risk such parasites might pose to sympatric species, for example the endangered Gilbert's potoroo which overlaps the range of the quokka in the far South West (Clark & Spencer 2006). The ongoing identification and characterisation of parasites has been an important focus and a recent review has demonstrated the importance of understanding the conservation implications of parasite diversity, both within species and more broadly at the level of ecosystems (Thompson et al. 2010).

Captive breeding of individuals for reintroduction requires a high level of care to ensure that disease is not introduced to wild populations. For example, Cryptosporidium muris infection detected in captive-bred bilbies was most likely acquired from mice by faecal contamination of food and water (Warren et al. 2003). Viral infections, too, have been identified and may be hampering conservation attempts. A bandicoot papillomatosis carcinomatosis virus that causes lesions and may have a severe impact on locomotion, sight or feeding, has been described in some wild and captivebred populations of the endangered western barred bandicoot (Bennett et al. 2008; Woolford et al. 2009). Often, the impact of parasites and viruses is difficult to determine and it is often unknown to what extent the microbes and parasites found may be correlated with

population health. Polymicrobial infection in a high percentage of all three populations of Gilbert's potoroos directly affects the reproductive system, and while not systemic, is likely to have an impact of the fecundity of infected individuals (Vaughan-Higgins *et al.* 2011). The woylie population crashes since 2000 have led to extensive investigation through a range of disciplines including parasitology. While various parasites have been discovered no clear causal agent for the recent population crashes has been identified (Smith *et al.* 2008; Paparini *et al.* 2012).

CONCLUSIONS

The understanding of marsupial biology has risen exponentially over the last century and the Western Australian contribution has been substantial. The application of the knowledge derived from studies such as those highlighted in this review will drive future conservation attempts, as the pressure on our natural environment continues to rise. In addition to preserving our unique biota, the conservation of our marsupials also has the potential to help in the restoration of threatened ecosystems, as highlighted by a recent review of the role of digging mammals in ecosystem processes (Fleming *et al.* 2014). The success of conservation strategies also relies on the interest, engagement and support of the wider community. Hopefully the publication of reviews such as presented here will spark the collective imagination.

ACKNOWLEDGEMENTS

The invitation to produce this review has led me very much through a process of returning to my roots. I once again found myself sitting on the floor of the library, sifting through the ancient bound copies of the Zoological Record to follow the work of my distinguished zoological professors and those before them. I sincerely thank Don and Felicity Bradshaw, and Harriet Mills for their detailed reviews and thoughtful suggestions for the improvement of this manuscript. I am indebted to Wes Bancroft for his constant support and substantial critical reviews of early drafts, and my thanks also to Gavin Prideaux and Margaret Warburton for their careful reading and suggestions for improvement.

REFERENCES

- ALACS E, SPENCER P S, TORES P & KRAUSS S 2011. Population genetic structure of island and mainland populations of the quokka, *Setonix brachyurus* (Macropodidae): a comparison of AFLP and microsatellite markers. *Conservation Genetics* 12, 297–309.
- ALEXANDER W B 1918. A new species of marsupial of the subfamily Phalangerinae. *Journal and Proceedings of the Royal Society of Western Australia* 4, 31–36.
- Anon. 2010. Gilbert's potoroo translocations proving successful.http://www.dec.wa.gov.au/news/archives/327-department-of-environment-and-conservation/6073-gilberts-potoroo-translocations-proving-successful.html>.
- Anon. 2011. Gilbert's potoroo mainland move. http://www.dec.wa.gov.au/news/archives/327-department-of-environment-and-conservation/6767-gilberts-potoroomainland-move.html>.

- Anon. 2012. Return to Dryandra. http://www.dec.wa.gov.au/our-environment/science-and-research/animal-conservation-research/5773-return-to-dryandra.html.
- ARCHER M 1974. New information about the Quaternary distribution of the thylacine (Marsupialia, Thylacinidae) in Australia. *Journal of the Royal Society of Western Australia* 57, 43–50.
- ARCHER M 1976. The basicranial region of marsupicarnivores (Marsupialia), interrelationships of carnivorous marsupials, and affinities of the insectivorous marsupial peramelids. Zoological Journal of the Linnean Society 59, 217–322.
- ARCHER M & BAYNES A 1972. Prehistoric mammal faunas from two small caves in the extreme southwest of Western Australia. Journal of the Royal Society of Western Australia 55, 80–89.
- ARCHER M, CRAWFORD I M & MERRILEES D 1980. Incision, breakages and charring, some probably man-made, in fossil bones from Mammoth Cave, Western Australia. *Alcheringa* 4, 115–131.
- ARCHER M & KIRSCH J A W 1977. The case for the Thylacomyidae and Myrmecobiidae, Gill 1872, or why are marsupial families so extended? *Proceedings of the Linnean Society of New South Wales* 102, 18–25.
- Arrese C, Archer M & Beazley L D 2002. Visual capabilities in a crepuscular marsupial, the honey possum (*Tarsipes rostratus*): a visual approach to ecology. *Journal of Zoology* **256**, 151–158.
- Ashman R, Keast D, Stanley N F & Waring H 1975. The immunological responses of marsupials. *American Zoologist* 15, 155–166.
- Bakker H R & Bradshaw S D 1989. Rate of water turnover and electrolyte balance of an arid-zone marsupial, the spectacled hare wallaby (*Lagorchestes conspicillatus*) on Barrow Island. *Comparative Biochemistry and Physiology Part A: Physiology* 92, 521–529.
- BAKKER H R & MAIN A R 1980. Condition, body composition and total body water estimation in the quokka, *Setonix brachyurus* (Macropodidae). *Australian Journal of Zoology* 28, 395–406.
- Barker S & Barker J 1959. Physiology of the quokka. Journal of the Royal Society of Western Australia 42, 72–76.
- Bartholomew G A 1956. Temperature regulation in the macropod marsupial *Setonix brachyurus*. *Physiological Zoology* 29, 26–40.
- Bennett M D, Woolford L, O'Hara A J, Nicholls P K, Warren K S, Hulme-Moir K L & Clark P 2007. Hematologic characteristics of captive western barred bandicoots (*Perameles bongainville*) from Western Australia. *Veterinary Clinical Pathology* 36, 348–353.
- Bennett M D, Woolford L, O'Hara A J, Warren K S & Nicholls P K 2008. In situ hybridization to detect bandicoot papillomatosis carcinomatosis virus type 1 in biopsies from endangered western barred bandicoots (*Perameles bongainville*). Journal of General Virology 89, 419–423.
- Benshemesh J 2008. İtjaritjari, Notoryctes typhilops (Stirling, 1889). In: Van Dyck S & Strahan R (eds) The Mammals of Australia, pp. 412–413. Reed Holland Publishers, Sydney.
- Benshemesh J & Aplin K 2008. Kakarratul, *Notoryctes caurinns* (Thomas, 1920). *In:* Van Dyck S & Strahan R (eds) *The Mammals of Australia*, pp. 410–411. Reed Holland Publishers, Sydney.
- Benshemesh J & Johnson K 2003. Biology and conservation of marsupial moles (*Notoryctes*). *In*: Jones M, Dickman C & Archer M (eds) *Predators with ponches: the biology of carivorous marsupials*, pp. 464–474. CSIRO Publishing, Collingwood.
- Bentley P J 1955. Some aspects of the water metabolism of an Australian marsupial *Setonix brachynrus*. *Journal of Physiology* 127, 1–10.
- Bentley P J & Shield J 1962. Metabolism and kidney function in the pouch young of the macropod marsupial *Setonix* brachynrus. Journal of Physiology 164, 127–137.

- Bester A J & Rusten K 2009. Trial translocation of the numbat (Myrmecobius fasciatus) into arid Australia. Australian Mammalogy 31, 9.
- Bradley A J 2003. Stress, hormones and mortality in small carnivorous marsupials. *In:* Jones M, Dickman C & Archer M (eds) *Predators with pouches: the biology of carivorous marsupials*, pp. 254–267. CSIRO Publishing, Collingwood.
- Bradley A J, Foster W K & Taggart D A 2008. Red-tailed phascogale, *Phascogale calura* (Gould, 1844). *In*: Van Dyck S & Strahan R (eds) *The Mammals of Australia*, pp. 101–102. Reed Holland Publishers, Sydney.
- Bradshaw D & Bradshaw F 2012. The physiology of the honey possum, *Tarsipes rostratus*, a small marsupial with a suite of highly specialised characters: a review. *Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology* 182, 469–489.
- Bradshaw F J & Bradshaw D 2011. Progesterone and reproduction in marsupials: a review. General and Comparative Eudocrinology 170, 18–40.
- Bradshaw F J, Stead-Richardson E J, Reeder A J, Oates J E & Bradshaw S D 2004. Reproductive activity in captive female honey possums, *Tarsipes rostratus*, assessed by faecal steroid analysis. *General and Comparative Endocrinology* **138**, 20–31.
- Bradshaw S D 1983a. Recent endocrinological research on the Rottnest Island quokka. *Journal of the Royal Society of Western* Australia 66, 55–61.
- Bradshaw S D, McDonald I R, Halinal R & Heller H 1978. Synthesis of progesterone by the placenta of a marsupial. *Journal of Endocrinology* 65, 451–452.
- Bradshaw S D E 1983b. Research on Rottnest Island. Journal of the Royal Society of Western Australia 66, 1–61.
- Burblidge A 2008a. Bettongia pusilla. In: 2008 Red List of Threatened Species, Version 2012.2.
- BURBIDGE A, DICKMAN C & JOHNSON K. 2008c. Chaeropus ecaudatus. In: IUCN 2008 Red List of Threatened Species. Version 2013.1.
- Burbidge A, Johnson K & Dickman C 2008a. *Macrotis leucura*. *In:* IUCN 2008 Red List of Threatened Species. Version 2013.1.
- Burbidge A A 2008b. Crescent nailtail wallaby, *Onychogalea lunata* (Gould, 1841). *In:* Van Dyck S & Strahan R (eds) *The Mammals of Australia*, pp. 357–359. Reed Holland Publishers, Sydney.
- Burbidge A A, Johnson K A, Fuller P J & Affken P F 2008b. Central hare-wallaby, *Lagorchestes asomatus* (Finlayson, 1943). *In:* Van Dyck S & Strahan R (eds) *The Mammals of Australia*, pp. 312–313. Reed Holland Publishers, Sydney.
- Burbidge A A and Johnson P M 2008. Spectacled hare-wallaby, Lagorchestes conspicillatus (Gould, 1842). Iu: Van Dyck S & Strahan R (eds) The Mammals of Australia, pp. 314–316. Reed Holland Publishers, Sydney.
- Burbidge A A & McKenzie N L 1989. Patterns in the modern decline of Western Australia's vertebrate fauna: causes and conservation implications. *Biological Conservation* **50**, 143–198.
- Burbidge A A, McKenzie N L & Fuller P J 2008d. Long-tailed dunnart, *Sminthopsis longicaudata* (Spencer, 1909). *In:* Van Dyck S & Strahan R (eds) *The Mammals of Australia*, pp. 148–150. Reed Holland Publishers, Sydney.
- Burbidge A A & Short J C 2008. Burrowing bettong, Bettongia lesneur (Quoy and Gaimard, 1824). In: Van Dyck S & Strahan R (eds) The Manmals of Australia, pp. 288–290. Reed Holland Publishers, Sydney.
- Burbidge A A & Webb M J 2008. Scaley-tailed possum, Wyulda squamicaudata (Alexander, 1919). In: Van Dyck S & Strahan R (eds) The Manmals of Australia, pp. 277–278. Reed Holland Publishers, Sydney.
- Burnett S 2008 Common planigale, *Planigale maculata* (Gould, 1851). *In*: Van Dyck S & Strahan R (eds) *The Mammals of Australia*, pp. 112–113. Reed Holland Publishers, Sydney.
- CAKE M H, OWEN F J & BRADSHAW S D (1980) Difference in the concentration of progesterone in plasma between pregnant

- and nonpregnant quokkas (Setonix brachyurus). Journal of Endocrinology 84, 153–158.
- Calaby J H 1957. A new record of the scaly-tailed possum (Wyulda squamicavdata Alexander). West Australian Naturalis, 5, 186–191.
- Calaby J H 1960. The numbat of south-western Australia. Australian Museum Magazine 13, 143–146.
- Calver M C & Dell J 1999. Conservation status of mammals and birds in southwestern Australian forests. I. Is there evidence of direct links between forestry practices and species decline and extinction? *Pacific Conservation Biology* 4, 296.
- Carthew S M & Bos D G 2008. Southern ningaui, Ningaui yvonneae (Kitcher, Stoddart and Henry, 1983). In: Van Dyck S & Strahan R (eds) The Manmals of Australia, pp. 120–121. Reed Holland Publishers, Sydney.
- Carthew S M, Cadzow B R & Foulkes J N 2008 Western pygmyspossum, Cercertetus conciunus (Gould, 1845). Iu: Van Dyck & Strahan R (eds) The Manmals of Australia, pp. 215–216, Reed Holland Publishers, Sydney.
- CLANCY T F & CROFT D B 2008. Common wallaroo, *Macropus robustus* (Gould, 1841). *In*: Van Dyck S & Strahan R (eds) *The Manimals of Australia*, pp. 346–348. Reed Holland Publishers, Sydney.
- CLARK P & Spencer P B S 2006. Haematological characteristics of wild quokka (Setonix brachyurus). Comparative Clinical Pathology 15, 82–86.
- CLARKE J, WARREN K, ROBERTSON I, CALVER M & DE TORES P 2008. Health and survival of translocated western ringtail possums. In: Glen A S (ed.) Proceedings of the 21st Australasian Wildlife Management Society Conference, p. 134. http://www.awms.org.au/assets/docs/Proceedings/awms08proceedings_fremantlewa.pdf.
- COOPER C E & GEISER F 2008. The "minimal boundary curve for endothermy" as a predictor of heterothermy in mammals and birds: a review. Journal of Comparative Physiology. B, Biochemical, Systemic, and Environmental Physiology 178, 1–8.
- COOPER C E & WITHERS P C 2004. Patterns of body temperature variation and torpor in the numbat, Myrmecobius fasciatus (Marsupialia: Myrmecobiidae). Journal of Thermal Biology 29, 277–284.
- Cooper N K 2008. Rory's pseudantechius, *Pseudantechinus roryi* (Cooper, Aplin and Adams, 2000). *In*: Van Dyck S & Strahan R (eds) *The Mammals of Australia*, pp. 75–76. Reed Holland Publishers, Sydney.
- CORBETT L K 1975. Geographic distribution and habitat of the marsupial mole, *Notoryctes typhlops. Australian Mammalogy* 1, 375–378.
- Coulson G 2008. Western grey kangaroo, *Macropus fuliginosus* (Desmarest, 1817). *In:* Van Dyck S & Strahan R (eds) *The Mammals of Australia*, pp. 333–334. Reed Holland Publishers, Sydney.
- COURTENAY J & FRIEND T 2004. Gilbert's potoroo (*Potorous gilbertii*) recovery plan, June 2003–June 2008. *Wildlife Management Plan* 32. Department of Conservation and Land Management, Perth.
- Cowing J A, Arrese C A, Davies W L, Beazley L D & Hunt D M 2008. Cone visual pigments in two marsupial species: the fattailed dunnart (Smiuthopsis crassicaudata) and the honey possum (Tarsipes rostratus). Proceedings of the Royal Society B-Biological Sciences 275, 1491–1499.
- CROFT D B & CLANCY T F 2008. Red kangaroo, *Macropus rufus* (Desmarest, 1822). *In:* Van Dyck S & Strahan R (eds) *The Mannuals of Australia*, pp. 352–354. Reed Holland Publishers, Sydney.
- CROWTHER M S 2008. Yellow-footed antechinus, Antechinus flavipes (Waterhouse, 1838). In: Van Dyck S & Strahan R (eds) The Mammals of Australia, pp. 86–88. Reed Holland Publishers, Sydney.
- DE TORES P J 2008a. Quokka, Setonix brachyurus (Quoy and

- Gaimard, 1830). *In:* Van Dyck S & Strahan R (eds) *The Manmals of Australia*, pp. 402–404. Reed Holland Publishers, Sydney.
- DE TORES P J 2008b. Western ringtail possum, *Pseudocheirus occidentalis* (Thomas, 1888). *In*: Van Dyck S & Strahan R (eds) *The Mamnuals of Australia*, pp. 253–255. Reed Holland Publishers, Sydney.
- DE TORES P J, HAYWARD M W, DILLON M J & BRAZELL R I 2007. Review of the distribution, causes for the decline and recommendations for management of the quokka, Setonix brachyurus (Macropodidae: Marsupialia), an endemic macropodid marsupial from south-west Western Australia. Conservation Science Western Australia 6, 13–73.
- DE TORES P J & START A N 2008. Woylie, Bettongia penicillata (Gray, 1837). In: Van Dyck S & Strahan R (eds) The Mannuals of Australia, pp. 291–292. Reed Holland Publishers, Sydney.
- DICKMAN C R 2008. Grey-bellied dunnart, Smithopsis griseoventer (Kitchener, Stoddart and Henry, 1984). In: Van Dyck S & Strahan R (eds) The Manimals of Australia, pp. 141–143. Reed Holland Publishers, Sydney.
- Dundas S, Adams P & Fleming P A 2012. Recovery of quokka (Setonix brachyurus) populations in southwestern Australia. In: 58th Scientific Meeting Australian Mammal Society, 2012, Port Augusta, Australia. http://researchrepository.murdoch.edu.au/15387/1/quokka_recovery.pdf.
- Dunlop J N, Cooper N K & Teale R J 2008. Pilbara ningaui, Ningaui timealeyi (Archer, 1975). In: Van Dyck S & Strahan R (eds) The Manmals of Australia, pp. 119–120. Reed Holland Publishers, Sydney.
- Dunnet G M 1962. A population study of the quokka, *Setonix brachynrus* Quoy & Gaimard (Marsupialia). II. Habitat, movements, breeding, and growth. *Wildlife Research* 7, 13–32.
- Dunnet G M 1963. A population study of the quokka, Setonix brachyurus Quoy & Gaimard (Marsupialia). III. The estimation of population parameters by means of the recapture technique. Wildlife Research 8, 78–117.
- ELDRIDGE M D B, KING J M, LOUPIS A K, SPENCER P B S, TAYLOR A C, POPE L C & HALL G P 1999. Unprecedented low levels of genetic variation and inbreeding depression in an island population of the black-footed rock wallaby. *Conservation Biology* 13, 531–541.
- ELDRIDGE M D B, KINNEAR J E, ZENGER K R, MCKENZIE L M & SPENCER P B S 2004. Genetic diversity in remnant mainland and "pristine" island populations of three endemic Australian macropodids (Marsupialia): Macropus eugeuii, Lagorchestes hirsutus and Petrogale lateralis. Conservation Genetics 5, 325–338.
- ELDRIDGE M D B & PEARSON D J 2008. Black-footed rock-wallaby, Petrogale lateralis (Gould, 1842). In: Van Dyck S & Strahan R (eds) The Manmals of Australia, pp. 376–380. Reed Holland Publishers, Sydney.
- ELDRIDGE M D B & TELFER W R 2008. Short-eared rock-wallaby, Petrogale brachyotis (Gould, 1841). In: Van Dyck S & Strahan R (eds) The Mawmals of Australia, pp. 365–366. Reed Holland Publishers, Sydney.
- ENDERS A C & ENDERS B K 1969. The placenta of the four-eyed opossum (*Philander opossum*). Anatomical Record 165, 431–450.
- FISHER A 2008. Long-tailed planigale, *Planigale ingrami* (Thomas, 1906). *In:* Van Dyck S & Strahan R (eds) *The Manimals of Australia*, pp. 110–111. Reed Holland Publishers, Sydney.
- FLANNERY T 1983. Revision of the macropodid subfamily Sthenurinae (Marsupialia; Macropodoidea) and the relationships of the species of *Troposodon* and *Lagostrophus*. Australian Manmalogy 6, 15–28.
- FLEAY D 1952. The Numbat: a passing relic of the earth's early furred animals. Ill. *Loud News* 221, 32–33.
- FLEMING P A, VALENTINE L E, BRETZ M R, PRENDERGAST A S, ANDERSON H & HARDY G E ST J 2014. Is the loss of Australian digging mammals contributing to a deterioration in ecosystem function? *Manumal Review* 44, 94–108.

- FLETCHER T & MORRIS K 2003. Captive breeding and predator control: a successful strategy for conservation in Western Australia. *In*: Holt W V, Pickard A R, Rodger J C & Wildt D E (eds) *Reproductive science and integrated conservation*, pp. 232–248. Cambridge University Press, Cambridge.
- FLYNN T T 1923. The yolk-sac and allantoic placenta in *Perameles*. *Quarterly Journal of Microscopical Science* 67, 123–182.
- FOULKES J N 2008. Ooldea dunnart, Sminthopsis ooldea (Troughton, 1965). In: Van Dyck S & Strahan R (eds) The Mannuals of Australia, pp. 154–156. Reed Holland Publishers, Sydney.
- Fraser E H & Kinnear J E 1969. Urinary creatinine excretion by macropod marsupials. Comparative Biochemistry and Physiology 28, 685–692.
- FRIEND G & WAYNE A 2003. Relationships between mammals and fire in south-west Western Australian ecosystems: what we know and what we need to know. In: Abbott I & Burrows N (eds.) Fire in ecosystems of south-west Western Australia: impacts and management. Symposium proceedings (Volume I), Perth, Australia, 16-18 April 2002, pp. 363–380.
- FRIEND G R & PEARSON D J 2008. Little long-tailed dunnart,
 Sminthopsis dolichura (Kitchener, Stoddart and Henry, 1984).
 In: Van Dyck S & Strahan R (eds) The Mammals of Australia,
 pp. 134–135. Reed Holland Publishers, Sydney.
- FRIEND J A 2008a. Gilbert's potoroo, Potorous gilbertii (Gould, 1841). In: Van Dyck S & Strahan R (eds) The Mammals of Australia, pp. 297–298. Reed Holland Publishers, Sydney.
- FRIEND J A 2008b Numbat, Myrmecobius fasciatus (Waterhouse, 1836). In: Van Dyck S & Strahan R (eds) The Manmals of Australia, pp. 162–165. Reed Holland Publishers, Sydney.
- FRIEND J A 2008c. Western barred bandicoot, Perameles bongaiuville (Quoy and Gaimard, 1824). In: Van Dyck S & Strahan R (eds) The Manunals of Australia, pp. 182–184. Reed Holland Publishers, Sydney.
- FRIEND T., BURBIDGE A & MORRIS K 2008a. Parautechinus apicalis. In: IUCN 2008 Red List of Threatened Species. Version 2013.1.
- FRIEND T, MORRIS K & VAN WEENAN J 2008b. Macrotis lagotis. In: IUCN 2008 Red List of Threatened Species. Version 2013.1.
- Fumagalli L, Moritz C, Taberlet P & Friend J A 1999. Mitochondrial DNA sequence variation within the remnant populations of the endangered numbat (Marsupialia: Myrmecobiidae: Myrmecobius fasciatus). Molecular Ecology 8, 1545–1549.
- Geiser F. 1994. Hibernation and daily torpor in marsupials: a review. Australian Journal of Zoology 42, 1–16.
- GLAUERT L 1910. The Mammoth Cave. Records of the Western Australian Museum and Art Gallery 1, 11–36.
- GLAUERT L 1912. The Mammoth Cave (continued). Records of the Western Australian Museum and Art Gallery 1, 39–46.
- GLAUFRT L 1914. The Mammoth Cave (continued). Records of the Western Australian Museum and Art Gallery 1, 244–251.
- GLAUERT L 1921. Pleistocene fossil vertebrates from Fitzroy River, West Kimberley, W.A. Journal and Proceedings of the Royal Society of Western Australia 7, 85–86.
- GLAUERT L 1926. Fossil Mammalia of Western Australia. Geological Survey of Western Australia Bulletin 88, 70–71.
- GLAUERT L 1929. Appendix. Note on the habits of Tarsipes spenserue Gray. Journat of the Royat Society of Western Australia 15, 15–16.
- GLAUERT L 1948. The cave fossils of the south-west. West Australian Naturalist 1, 100–104.
- GLAUERT L 1950. The development of our knowledge of the marsupials of Western Australia. *Journal of the Royal Society of Western Australia* 34, 115–134.
- GORDON G 2008a. Desert bandicoot, Peraneles eremiana (Spencer, 1897). In: Van Dyck S & Strahan R (eds) The Mammals of Australia, pp. 185–186. Reed Holland Publishers, Sydney.

- GORDON G 2008b. Northern brown bandicoot, Isoodon macronrus (Gould, 1842). In: Van Dyck S & Strahan R (eds) The Manmals of Australia, pp. 178–180. Reed Holland Publishers, Sydney.
- GORDON G & HULBERT A J 1989. Peramelidae. *In:* Walton D W R & Richardson B J (eds) *Fauna of Australia. Manunalia. Vol. 1B*, pp. 603–624. Australian Government Publishing Service, Canberra.
- GROOM C 2010. Justification for continued conservation efforts following the delisting of a threatened species: a case study of the woylie, *Bettongia penicillata ogilbyi* (Marsupialia: Potoroidae). *Wildlife Research* 37, 183–193.
- HARDMAN B & MORO D 2006. Optimising reintroduction success by delayed dispersal: is the release protocol important for hare-wallabies? *Biological Conservation* 128, 403–411.
- Hayward M W, de Tores P J, Dillon M J & Fox B J 2003. Local population structure of a naturally occurring metapopulation of the quokka (Setonix brachyurus Macropodidae: Marsupialia). Biological Conservation 110, 343–355.
- Heap R B, Renfree M B & Burton R D 1980. Steroid metabolism in the yolk sac placenta and endometrium of the tammar wallaby, *Macropus engenii*. *Journal of Endocrinology* 87, 399–349.
- Heller H 1973. The effects of oxytocin and vasopressin during the oestrus cycle and pregnanct of the uterus of a marsupial species, the quokka (Setonix brachynrus). Journal of Endocrinology 58, 657–671.
- HILL J P 1900. On the foetal membranes, placentation and parturition of the native cat (Dasyurus viverrinus). Anatomischer Anzeiger 18, 364–373.
- HINDS L A 2008. Tammar wallaby, Macropus eugenii (Desmarest, 1817). In: Van Dyck S & Strahan R (eds) The Manimals of Australia, pp. 330–332. Reed Holland Publishers, Sydney.
- HINDS L A & TYNDALE-BISCOE C H 1982. Plasma progesterone levels in the pregnant and non-pregnant tammar Macropus eugenii. Journal of Endocrinology 93, 99–107.
- How R A, Spencer P B S & Schmitt L H 2009. Island populations have high conservation value for northern Australia's top marsupial predator ahead of a threatening process. *Journal of Zoology* 278, 206–217.
- Hume 1 D 1999. Marsupial nutrition. Cambridge University Press, Cambridge.
- INGLEBY S & GORDON G 2008. Northern nailtail wallaby, Onychogalea unguifera (Gould, 1841) In: Van Dyck S & Strahan R (eds) The Manunals of Australia, pp. 359–361. Reed Holland Publishers, Sydney.
- IUCN (International Union for Conservation of Nature) 2012. IUCN Red List of Threatened Species. Version 2012.2. http://www.inaturalist.org/taxon_schemes/14>.
- JENKINS C F H 1974. The decline of the dalgite (Macrotis lagotis) and other wildlife in the Avon Valley. Western Australian Naturalist 12, 169–172.
- JOHNSON C N & ISAAC J L 2009. Body mass and extinction risk in Australian marsupials: the 'Critical Weight Range' revisited. Austral Ecology 34, 35–40.
- JOHNSON K A 2008a. Bilby, Macrotis lagotis (Reid, 1837). In: Van Dyck S & Strahan R (eds) The Mannuals of Australia, pp. 191– 193. Reed Holland Publishers, Sydney.
- JOHNSON K A 2008b. Lesser bilby, Macrotis leucura (Thomas, 1887). In: Van Dyck S & Strahan R (eds) The Mammals of Australia, pp. 194–195. Reed Holland Publishers, Sydney.
- JOHNSON K A & BURBIDGE A A 2008a. Pig-footed bandicoot, Chaeropus ecandatus (Ogilby, 1838). In: Van Dyck S & Strahan R (eds) The Mammals of Australia, pp. 172–173. Reed Holland Publishers, Sydney.
- JOHNSON K A & BURBIDGE A A 2008b. Rufous hare-wallaby, Lagorchestes lirisutus (Gould, 1844). In: Van Dyck S & Strahan R (eds) The Mammals of Australia, pp. 317–319. Reed Holland Publishers, Sydney.
- Kerle J A & How R A 2008. Common brushtail possum, Trichosurus vulpecula (Kerr, 1792). In: Van Dyck S & Strahan

- R (eds) *The Mammals of Australia*, pp. 274–276. Reed Holland Publishers, Sydney.
- KINNEAR A & SHIELD J W 1975. Metabolism and temperature regulation in marsupials. Comparative Biochemistry and Physiology Part A: Physiology 52, 235–245.
- KINNEAR J E & MAIN A R 1975. The recycling of urea nitrogen by the wild tammar wallaby (Macropus eugenii); a "ruminantlike" marsupial. Comparative Biochemistry and Physiology Part A: Physiology 51, 793–810.
- Kinnear J E, Onus M L & Bromilow R N 1988. Fox control and rock-wallaby population dynamics. *Australian Wildlife Research* 15, 435–450.
- KINNEAR J E, PUROHIT K G & MAIN A R 1968. The ability of the tammar wallaby (*Macropus eugenii*, Marsupialia) to drink sea water. Comparative Biochemistry and Physiology 25(3), 761–782.
- KITCHENER D J 1972. The importance of shelter to the quokka, Setonix brachyurus (Marsupialia), on Rottnest Island. Australian Journal of Zoology 20, 281–299.
- KITCHENER D J 1973. Notes on home range and movement in two small macropods, the potoroo (*Potorous apicalis*) and the quokka (*Setonix brachyurus*). *Manunalia* 37, 231–240.
- Kitchener D J & Friend J A 2008. Broad-faced potoroo, *Potorous platyops* (Gould, 1844). *In*: Van Dyck S & Strahan R (eds) *The Mammals of Australia*, pp. 301–302. Reed Holland Publishers, Sydney.
- KITCHENER D J & SANSON G D 1978. Petrogale burbidgei (Marsupialia: Macropodidae), a new rock wallaby from the Kimberley, Western Australia. Records of the Western Australian Museum 6, 269–285.
- LAMBERT C & MILLS H 2006. Husbandry and breeding of the Dibbler Paranteclinus apicalis at Perth Zoo. International Zoo Yearbook 40, 290–301.
- LOWRY D C & LOWRY J W J 1967. Discovery of a thylacine (Tasmanian tiger) carcase in a cave near Eucla. *Helictite* 5, 25–29.
- Lowry J W J & Merriles D 1969. Age of the desiccated carcase of a thylacine (Marsupialia, Dasyuroidea) from Thylacine Hole, Nullarbor Region, Western Australia. *Helictite* 7, 15–16.
- LUNDELIUS E L J 1963. Vertebrate remains from the Nullarbor Caves, Western Australia. Journal of the Royal Society of Western Australia 46, 75–80.
- Lundelius E L J & Turnbull W D 1973. The mammalian fauna of the Madura Cave, Western Australia. Part 1. Fieldiana: Geology 31, 1–35.
- Lundeljus E L J & Turnbull W D 1981. The mammalian fauna of the Madura Cave, Western Australia. Part IV: Peramelids. Fieldiana: Geology (New Series) 6, 1–71.
- Main A R 1961. The occurrence of Macropodidae on islands and its climatic and ecological implications. *Journal of the Royal Society of Western Australia* 44, 84–89.
- MAIN A R 1968. Physiology in the management of kangaroos and wallabies. *Proceedings of the Ecological Society of Australia* 3, 96–105.
- MAIN A R 1983. Macropod physiology: a possible integration with ecological and evolutionary studies. *Journal of the Royal Society of Western Australia* 68, 5–9.
- MAIN A R & YADAV M 1971. Conservation of macropods in reserves in Western Australia. Biological Conservation 3, 123– 133.
- Masters P 2008. Crest-tailed mulgara, Dasycercus cristicauda (Kreft, 1867). In: Van Dyck S & Strahan R (eds) The Manunals of Australia, pp. 49–50. Reed Holland Publishers, Sydney.
- McCrady E 1938. The embryology of the opossum. *American Anatomical Memoirs* 16, 1–233.
- McKenzie N L & Cole J R 2008. Lesser hairy-footed dunnart, Sminthopsis youngsoni (McKenzie and Archer, 1982). In: Van Dyck S & Strahan R (eds) The Mamnals of Australia, pp. 160– 161. Reed Holland Publishers, Sydney.
- McKenzie N L & Dickman C R 2008. Wongai ningaui, Ningani

- ridei (Archer, 1975). In: Van Dyck S & Strahan R (eds) The Mammals of Australia, pp. 117–118. Reed Holland Publishers, Sydney.
- McKenzie N. L. & Kitchener D. J. 2008. White-tailed dunnart, *Sminthopsis granulipes* (Troughton, 1932). *In:* Van Dyck S. & Strahan R. (eds) *The Mammals of Australia*, pp. 140–141. Reed Holland Publishers, Sydney.
- McKenzie N L, Morris K D & Dickman C R 2008. Golden bandicoot, *Isoodon auratus* (Ramsay, 1887). *In*: Van Dyck S & Strahan R (eds) *The Mammals of Australia*, pp. 176–178. Reed Holland Publishers, Sydney.
- Merchant J C 1979. The effect of pregnancy on the interval between one oestrus and the next in the tammar wallaby, Macropus eugenii. Journal of Reproduction and Fertility 56, 459–463.
- MERCHANT J C 2008. Agile wallaby, Macropus agilis (Gould, 1842).
 In: Van Dyck S & Strahan R (eds) The Mammals of Australia, pp. 323–324. Reed Holland Publishers, Sydney.
- Merrilees D 1965. Two species of the extinct genus Sthenurus Owen (Marsupialia, Macropodidae) from south-eastern Australia, including Sthenurus filli sp. nov. Journal of the Royal Society of Western Australia 48, 22–32.
- MERRILEES D 1967. South-western Australian occurrences of Sthenurus (Marsupialia, Macropodidae), including Sthenurus brownei sp. nov. Journal of the Royal Society of Western Australia 50, 65–79.
- Merrilees D 1968. Man the destroyer: late Quaternary changes in Australian marsupial fauna. *Journal of the Royal Society of Western Australia* 51, 1–24.
- Merrilees D 1970a. A check on the radiocarbon dating of desiccated thylacine (marsupial 'wolf') and dog tissue from Thylacine Hole, Nullarbor region, Western Australia. *Helictite* 8, 39–42.
- Merrilees D 1970b. Two new fossil finds representing the large extinct diprotodontid marsupial *Zygomaturus*. The Western Australian Naturalist 11, 111–113.
- MILLS H & BENCINI R 2000. New evidence for facultative male die-off in island populations of dibblers, *Parantechinus apicalis*. Australian Journal of Zoology 48, 501–510.
- MILLS H R, Bradshaw F J, Lambert, C & Bradshaw S D 2012. Reproduction in the marsupial dibbler, *Parantechinus apicalis*; differences between island and mainland populations. *General and Comparative Endocrinology* 178, 347–354.
- MOIR R J, SOMERS M, SHARMAN G & WARING H 1954. Ruminant-like Digestion in a Marsupial. *Nature* 173, 269–270.
- MORCOMBE M K 1967. The rediscovery after 83 years of the dibbler *Anteclinus apicalis* (Marsupialia, Dasyuridae). *The Western Australian Naturalist* 10, 102–111.
- MORO D 2003. Translocation of captive-bred dibblers Parantechinus apicalis (Marsupialia: Dasyuridae) to Escape Island, Western Australia. Biological Conservation 111, 305– 315
- MORRIS K D & CHRISTENSEN P 2008. Western brush wallaby, Macropus irma (Jourdan, 1837). In: Van Dyck S & Strahan R (eds) The Mammals of Australia, pp. 340–341. Reed Holland Publishers, Sydney.
- MORRIS K D & MCKENZIE N L 2008. Gilbert's dunnart, Sminthopsis gilberti (Kitchener, Stoddart and Henry, 1984). In: Van Dyck S & Strahan R (eds) The Mammals of Australia, pp. 138–139. Reed Holland Publishers, Sydney.
- MORTON S R & DICKMAN C R 2008a. Fat-tailed dunnart, Sminthopsis crassicaudata (Gould, 1844). In: Van Dyck S & Strahan R (eds) The Mammals of Australia, pp. 132–133. Reed Holland Publishers, Sydney.
- MORTON S R & DICKMAN C R 2008b. Stripe-faced dunnart, Sminthopsis macroura (Gould, 1845). In: Van Dyck S & Strahan R (eds) The Manmals of Australia, pp. 150–152. Reed Holland Publishers, Sydney.
- MURRAY P and MEGIRIAN D 2000. Two new genera and three new species of Thylacinidea (Marsupialia) from the Miocene of

- the Northern Territory, Australia. The Beagle, Records of the Museums and Art Galleries of the Northern Territory 16, 145–162.
- Nicholls D G 1971. Daily and seasonal movements of the quokka, *Setonix brachyurus* (Marsupialia), on Rottnest Island. *Australian Journal of Zoology* 19, 215–226.
- Nilsson M A 2006. Phylogenetic relationships of the Banded Hare wallaby (*Lagostrophus fasciatus*) and a map of the kangaroo mitochondrial control region. *Zoologica Scripta* 35, 387–393.
- OAKWOOD M 2008. Northern quoll, *Dasyurus hallucatus* (Gould, 1842). *Iu*: Van Dyck S & Strahan R (eds) *The Mammals of Australia*, pp. 57–59. Reed Holland Publishers, Sydney.
- OATES J E, Bradshaw F J & Bradshaw S D 2004. The influence of photoperiod on the reproductive activity of female Honey possums, *Tarsipes rostratus* (Marsupialia: Tarsipedidae): assessed by faecal progestagens and oestradiol-17 beta. *General and Comparative Endocrinology* 139, 103–112.
- OATES J E, BRADSHAW F J, BRADSHAW S D, STEAD-RICHARDSON E J & PHILIPPE D L 2007. Reproduction and embryonic diapause in a marsupial: Insights from captive female Honey possums, *Tarsipes rostratus* (Tarsipedidae). *General and Comparative Endocrinology* **150**, 445–461.
- OWEN F J, CAKE M H & BRADSHAW S D 1982. Characterisation and properties of a progesterone receptor in the uterus of a marsupial (Setonix brachyurus). Journal of Endocrinology 93, 17–24.
- PACIONI C, WAYNE A F & SPENCER P B S 2011. Effects of habitat fragmentation on population structure and long-distance gene flow in an endangered marsupial: the woylie. *Journal of Zoology* 283, 98–107.
- Paparini A, Ryan U M, Warren K, McInnes L M, de Tores P & Irwin P J 2012. Identification of novel *Babesia* and *Theileria* genotypes in the endangered marsupials, the woylie (*Bettongia penicillata ogilbyi*) and boodie (*Bettongia lesueur*). Experimental Parasitology 131, 25–30.
- Parker W K 1890. On the skull of Tarsipes rostratus. Studies from the Museum of Zoology in University College Dundee 1, 79–84.
- Paull D J 2008. Southern brown bandicoot, *Isoodon obesulus* (Shaw, 1797). *In*: Van Dyck S & Strahan R (eds) *The Mammals of Australia*, pp. 180–182. Reed Holland Publishers, Sydney.
- Pearson D J, Burbidge A A, Lochman J & Start A N 2008. Monjon, *Petrogale burbidgei* (Kitchener and Sanson, 1978). *In:* Van Dyck S & Strahan R (eds) *The Mammals of Australia*, pp. 367–368. Reed Holland Publishers, Sydney.
- Pearson D J & Churchill S K 2008. Sandhill dunnart, *Sminthopsis psanmophila* (Spencer, 1985). *In:* Van Dyck S & Strahan R (eds) *The Mammals of Australia*, pp. 156–158. Reed Holland Publishers, Sydney.
- PEARSON D J & ELDRIDGE M D B 2008. Rothschild's rock-wallaby, Petrogale rothschildi (Thomas, 1904). In: Van Dyck S & Strahan R (eds) The Mammals of Australia, pp. 389–390. Reed Holland Publishers, Sydney.
- Pearson D J & McKenzie N L 2008. Hairy-footed dunnart, Sminthopsis hirtipes (Thomas, 1898). In: Van Dyck S & Strahan R (eds) The Manunals of Australia, pp. 143–145. Reed Holland Publishers, Sydney.
- POOLE W 1973. A study of breeding in grey kangaroos, *Macropus gigauteus* Shaw and *M. fuliginosus* (Desmarest), in central New South Wales. *Australian Journal of Zoology* 21, 183–212.
- PRIDEAUX G J 2004. Systematics and evolution of the sthenurine kangaroos. *University of California Publications in Geological Sciences* 146.
- PRIDEAUX G J, AYLIFFE L K, DESANTIS L R G, SCHUBERT B W, MURRAY P F, GAGAN M K & CERLING T E 2009. Extinction implications of a chenopod browse diet for a giant Pleistocene kangaroo. Proceedings of the National Academy of Sciences 106, 11646–11650.
- PRIDEAUX G J, LONG J A, AYLIFFE L K, HELLSTROM J C, PILLAMS B, BOLES W E, HUTCHINSON M N, ROBERTS R G, CUPPER M L,

- Arnold L. J., Devine P. D. & Warburton N. M. 2007a. An aridadapted middle Pleistocene vertebrate fauna from south-central Australia. *Nature* 445, 422–425.
- PRIDEAUX G J, ROBERTS R G, MEGIRIAN D, WESTAWAY K E, HELLSTROM J C & OLLEY J M 2007b. Mammalian responses to Pleistocene climate change in southeastern Australia. *Geology* 35, 33–36.
- PRIDEAUX G J & WARBURTON N M 2008. A new fossil treekangaroo (Diprotodontia: Macropodidae) from the Nullarbor Plain of South-Central Australia. *Journal of Vertebrate Paleontology* 28, 463–478.
- PRIDEAUX G J & WARBURTON N M 2009. Bolira nullarbora sp. nov., a second tree-kangaroo (Marsupialia: Macropodidae) from the Pleistocene of the Nullarbor Plain, Western Australia. Records of the Western Australian Museum 25, 165–179.
- PRIDEAUX G J & WARBURTON N M 2010. An osteology-based appraisal of the phylogeny and evolution of kangaroos and wallabies (Macropodidae: Marsupialia). Zoological Journal of the Linnean Society 159, 954–987.
- PRINCE R I T & RICHARDS J D 2008. Banded hare-wallaby, Lagostrophus fasciatus (Peron and Lesueur, 1807). In: Van Dyck S & Strahan R (eds) The Manimals of Australia, pp. 407–408. Reed Holland Publishers, Sydney.
- Renfree M 2008. Honey possum, *Tarsipes rostratus* (Gervais and Verreaux, 1842). *In*: Van Dyck S & Strahan R (eds) *The Mammals of Australia*, pp. 258–260. Reed Holland Publishers, Sydney.
- Renfree M B 1980. Embryonic diapause in the honey possum Tarsipes spencerae, Search 11, 81.
- RENFREE M B, RUSSELL E M & WOOLLER R D 1984. Reproduction and life history of the honey possum *Tarsipes rostratus*. *In*: Smith A P & Hume I D (eds) *Possums and Gliders*, pp. 427–437. Australian Mammal Society, Sydney.
- RENFREE M B & SHAW G 2000. Diapause. Annual Review of Physiology 62, 353–353.
- RICHAROSON K C, WOOLLER R D & COLLINS B G 1986. Adaptation to a diet of nectar and pollen in the marsupial *Tarsipes* rostratus (Marsupialia, Tarsipedidae). *Journal of Zoology* 208, 285–297.
- RIDE W D L 1957. Protemnodon parma (Waterhouse) and the classification of related wallabies (Protemnodon, Thylagale and Setonix). Proceedings of the Zoological Society of London 128, 327–346.
- RIDE W D L 1959. Mastication and taxonomy in the macropodine skull: function and taxonomic importance. Systematics Association Publication 3, 33–59.
- RIDE W D L 1961. The cheek-teeth of Hypsiprynmodon moschatus Ramsay 1876 (Macropodidae: Marsupialia). Journal of the Royal Society of Western Australia 40, 53–60.
- RIDE W D L 1962. On the use of generic names for kangaroos and wallabies (subfamily Macropodinae). *Australian Journal of Science* 24, 367–372.
- RIOE W D L 1971a. Marsupial geography. Brookfield Bandarlog 38, 3–6.
- RIDE W D L 1971b. On the fossil evidence of the evolution of the Macropodidae. *Australian Zoologist* 16, 6–16.
- RIDE W D L 1979. The Macropodidae. Australian Mammalogy 2, 1–14.
- RIDE W D L & SERVENTY D L 1963. The fauna of Western Australia. Official Year Book of Western Australia 1962, 60–72.
- RISBEY D A, CALVER M C & SHORT J 1997. Control of feral cats for Nature Conservation. 1. Field tests fo four baiting methods. Wildlife Research 24, 319–326.
- RITCHIE E G 2008. Antilopine wallaroo, Macropus antilopinus (Gould, 1842). In: Van Dyck S & Strahan R (eds) The Manmals of Australia, pp. 325–326. Reed Holland Publishers, Sydney.
- ROBERTS R G, FLANNERY T F, AYLIFFE L K, YOSHIDA H., OLLEY J M, PRIDEAUX G J, LASLETT G M, BAYNES A, SMITH M A, JONES R & SMITH B L 2001. New ages for the last Australian megafauna:

- continent-wide extinction about 46,000 years ago. Science 292, 1888–1892.
- Rong J, Bunce M, Wayne A, Pacioni C, Ryan U & Irwin P 2012. A high prevalence of *Theileria penicillata* in woylies (*Bettongia penicillata*). Experimental Parasitology 131, 157–161.
- RUNCIE M J 1999. Movements, dens and feeding behaviour of the tropical scaly-tailed possum (Wyulda squamicaudata). Wildlife Research 26, 367–373.
- Sadleir R M F S & Tyndale-Biscoe C H 1977. Photoperiod and the termination of embryonic diapause in the marsupial *Macropus eugenii*. *Biology of Reproduction* **16**, 605–608.
- Sanson G D & Churchill S K 2008. Nabarlek, *Petrogale concinna* (Gould, 1842). *In*: Van Dyck S & Strahan R (eds) *The Mannuals of Australia*, pp. 370–371. Reed Holland Publishers, Sydney.
- SANSON G D, NELSON J E & FELL P 1985. Ecology of Peradorcas conciuna in Arnhem Land Australia in a wet and a dry season. Proceedings of the Ecological Society of Australia 13, 65– 72.
- Serena M & Soderquist T 2008. Western quoll, *Dasyurus geoffroii* (Gould, 1841). *In*: Van Dyck S & Strahan R (eds) *The Mannuals of Australia*, pp. 54–56. Reed Holland Publishers, Sydney.
- Serventy V 1962, The vanishing numbat of Australia. *Pacific Science* 15, 15–18.
- SHARMAN G 1955a. Studies on marsupial reproduction. 2. The oestrous cycle of Setonix brachyurus. Australian Journal of Zoology 3, 44–55.
- SHARMAN G 1955b. Studies on marsupial reproduction. 3. Normal and delayed pregnancy in Setonix brachyurus. Australian Journal of Zoology 3, 56–70.
- SHARMAN G 1970. Reproductive physiology of marsupials. Science 167, 1221–1228.
- SHAW G, RENFREE M & FLETCHER T P 1996. A role for glucocorticoids in parturition in a marsupial, *Macropus eugenii*. Biology of Reproduction 54, 728–733.
- SHIELD J 1964. A breeding season difference in two populations of the Australian macropod marsupial (*Setonix brachyurus*). *Journal of Mammalogy* 45, 616–625.
- SHIELD J 1968. Reproduction of the quokka, Setonix brachyurus, in captivity. Journal of Zoology 155, 427–444.
- Shield J W & Woolley P A 1963. Population aspects of delayed birth in the quokka (Setonix brachyurus). Proceedings of the Zoological Society of London 141, 783–791.
- SHORT J, BRADSHAW S D, GILES J, PRINCE R I T & WILSON G R 1992. Reintroduction of macropods (Marsupialia: Macropodoidea) in Australia—a review. Biological Conservation 62, 189–204.
- SHORT J & TURNER B 2005. Control of feral cats for nature conservation. IV. Population dynamics and morphological attributes of feral cats at Shark Bay, Western Australia. Wildlife Research 32, 489–501.
- Sinclair E A, Costello B, Courtenay J M & Crandall K A 2002.

 Detecting a genetic bottleneck in Gilbert's potoroo (*Potorous gilbertii*) (Marsupialia: Potoroidae), inferred from microsatellite and mitochondrial DNA sequence data. *Conservation Genetics* 3, 191–196.
- SLAVEN M R & RICHARDSON K C 1988. Aspects of the form and function of the kidney of the honey possum, Tarsipes rostratus. Australian Journal of Zoology 36, 465–471.
- SMITH A, CLARK P, AVERIS S, LYMBERY A J, WAYNE A F, MORRIS K D & THOMPSON R C A 2008. Trypanosomes in a declining species of threatened Australian marsupial, the brush-tailed bettong *Bettongia penicillata* (Marsupialia: Potoroidae). *Parasitology* 135, 1329–1335.
- SODERQUIST T & RHIND S 2008. Brush-tailed Phascogale, *Pliascogale tapoatafa* (Meyer, 1793). *In:* Van Dyck S & Strahan R (eds) *The Manumals of Australia*, pp. 105–107. Reed Holland Publishers, Sydney.
- SOROKIN L 1981. Adrenal function in the neonatal quokka, Setonix brachyurus. BSc (Hons) thesis, University of Western Australia, Perth (unpubl.).

- Springer M S, Westerman M, Kavanagh J R, Burk A, Woodburne W O, Kao D J & Krajewski C 1998. The origin of the Australian marsupial fauna and the phylogenetic affinities of the enigmatic moito del monte and marsupial mole. *Proceedings of the Royal Society, London (B)Biological Sciences* 265, 2381–2386.
- STANLEY N F 1983. Immunological studies on the quokka. *Journal of the Royal Society of Western Australia* 66, 28–31.
- STANLEY N F, YADAV M, WARING H & EADIE M 1972. The effect of thymectomy on response to various antigens of a marsupial Setonix brachyurus (quokka). Immunology and Cell Biology 50, 689–702.
- Stead-Richardson E, Bradshaw D, Friend T & Fletcher T 2010. Monitoring reproduction in the critically endangered marsupial, Gilbert's potoroo (*Potorous gilbertii*): preliminary analysis of faecal oestradiol-17β, cortisol and progestagens. *General and Comparative Endocrinology* 165, 155–162.
- STORR G M 1964. The environment of the quokka (Setonix brachyurus) in the Darling Range, Western Australia. Journal of the Royal Society of Western Australia 47, 1–2.
- Suckling G C 2008. Sugar glider, *Petaurus breviceps* (Waterhouse, 1839). *In*: Van Dyck S & Strahan R (eds) *The Mammals of Australia*, pp. 230–232. Reed Holland Publishers, Sydney.
- Sumner P, Arrese C A & Partridge J C 2005. The ecology of visual pigment tuning in an Australian marsupial: the honey possum *Tarsipes rostratus*. *Journal of Experimental Biology* 208, 1803–1815.
- TAGGART D A & TEMPLESMITH P D 2008. Southern hairy-nosed wombat, Lasiorlinus latifrons (Owen, 1845). In: Van Dyck S & Strahan R (eds) The Mammals of Australia, pp. 204–206. Reed Holland Publishers, Sydney.
- THOMAS O 1920. Notoryctes of north-west Australia. Annals and Magazine of Natural History (Series 9) 6, 111–113.
- THOMPSON R C A, LYMBERY A J & SMITH A 2010. Parasites, emerging disease and wildlife conservation. *International Journal for Parasitology* 40, 1163–1170.
- THOMPSON S A & THOMPSON G G 2009. A case for in situ management of Western Ringtail Possums, *Pseudocheirus occidentalis*, in development areas. *Journal of the Royal Society of Western Australia* 92, 269–276.
- Troughton E L G 1932. A revision of the rabbit-bandicoots. Family Peramelidae, Genus *Macrotis*. *Australian Zoologist* 7, 219–236.
- Tyndale-Biscoe C H 1965. The female urogenital system and reproduction of the marsupial *Lagostrophus fasciatus*. *Australian Journal of Zoology* 13, 255–267.
- TYNDALE-BISCOE C H 1978. Hormonal control of embryonic diapause and reactivation in the tammar wallaby. *In:* Whelan J (ed.) *Maternal recognition of pregnaucy*, pp. 173–190. Ciba Foundation Symposium **64**.
- Tyndale-Biscoe C H 1997. Marsupials and modern biology—breaking the paradigms. *In*: Saunders N & Kinds L (eds) *Marsupial biology: recent research, new perspectives,* pp. 1–19. University of New South Wales Press, Sydney.
- Tyndale-Biscoe C H 2001. Australasian marsupials—to cherish and to hold. *Reproduction, Fertility and Development* 13, 477–485.
- Tyndale-Biscoe C H 2005. Life of marsupials. CSIRO Publishing, Collingwood.
- Tyndale-Biscoe C H, Hearn J P & Renfree M B 1974. Control of reproduction in macropodid marsupials. *Journal of Endocrinology* 63, 589-614.
- Tyndale-Biscoe C H & Hinds L 1981. Hormonal control of the corpus luteum and embryonic diapause in macropodid marsupials. *Journal of Reproduction and Fertility Supplement* 29, 111–117.
- Valente A 2008. Kultarr, *Antechinomys laniger* (Gould, 1856). *In:* Van Dyck S & Strahan R (eds) *The Mammals of Australia*, pp. 122–124. Reed Holland Publishers, Sydney.
- VAUGHAN-HIGGINS R, BULLER N, FRIEND J A, ROBERTSON 1,

- MONAGHAN C L, FENWICK S & WARREN K 2011. Balanoposthitis, dyspareunia, and treponema in the critically endangered Gilbert's potoroo (*Potorous gilbertii*). *Journal of Wildlife Diseases* 47, 1019–1025.
- VOSE H M 1973. Feeding habits of the Western Australian honey possum, Tarsipes spenserae, Journal of Manmalogy 54, 245–247.
- WARBURTON N M 2006. Functional morphology of marsupial moles (Marsupialia: Notoryctidae). Verhandlungen des Naturwisseuschaftlichen Vereins in Hamburg 42, 39–149.
- WARBURTON N M 2009. Comparative jaw muscle anatomy in kangaroos, wallabies, and rat-kangaroos (Marsupialia: Macropodoidea). *The Anatomical Record* 292, 875–884.
- WARING H 1959. Introduction (to Rottnest Island: The Rottnest Biological Station and Recent Scientific Research). Journal of the Royal Society of Western Australia 42, 65–66.
- WARING H, MOIR R J & TYNDALE-BISCOE C H 1966. Comparative physiology of marsupials. Advances in Comparative Physiology and Biochemistry 2, 237–376.
- Waring H, Sharman G B, Lovat D & Kahan M 1955. Studies on marsupial reproduction. 1. General features and techniques. Australian Journal of Zoology 3, 34–43.
- WARREN K S, SWAN R A, MORGAN-RYAN U M, FRIEND J A & ELLIOT A 2003. Cryptosporidium muris infection in bilbies (Macrotis lagotis). Australian Veterinary Journal 81, 739–741.
- WAYNE A F, LIDDELOW G L & WILLIAMS M R 2011. Forestcheck: terrestrial vertebrate associations with fox control and silviculture in jarrah (Encalyptus marginata) forest. Anstralian Forestry 74, 336–349.
- WAYNE A F, MAXWELL M A, WARD C G, VELLIOS C V, WARO B G, LIDDELOW G L, WILSON I, WAYNE J C & WILLIAMS M R 2013. Importance of getting the numbers right: quantifying the rapid and substantial decline of an abundant marsupial, Bettongia penicillata. Wildlife Research 40, 169–183.
- WEBB M J, KERLE J A & WINTER J W 2008. Rock ringtail possum, Petropseudes dalıli (Collett, 1895). In: Van Dyck S & Strahan R (eds) The Mammals of Australia, pp. 243–244. Reed Holland Publishers, Sydney.
- Westerman M, Burk A, Amrine-Madsen H M, Prideaux G J, Case J A & Springer M S 2002. Molecular evidence for the last survivor of an ancient kangaroo lineage. *Journal of Mammalian Evolution* 9, 209–223.
- WHITE S R 1952. The occurrence of the quokka in the south-west. West Australian Naturalist 3, 101–103.
- WIENS D, RENFREE M & WOOLLER R O 1980. Pollen loads of honey possums (Tarsipes spenserae) and nonflying mammal pollination in southwestern Australia. Annals of the Missouri Botanical Garden 66, 830–838.
- WITHERS P C, COOPER C E & LARCOMBE A N 2006. Environmental correlates of physiological variables in marsupials. *Physiological and Biochemical Zoology* **79**, 437–453.
- WITHERS P C, RICHARDSON K C & WOOLLER R D 1990. Metabolic physiology of euthermic and torpid honey possums, *Tarsipes rostratus*. Australian Journal of Zoology 37, 685–693.
- WITHERS P C, THOMPSON G G & SEYMOUR R S 2000. Metabolic physiology of the northwestern marsupial mole, *Notoryctes caurinus* (Marsupialia: Notoryctidae). *Australiau Journal of Zoology* 48, 241–258.
- WOOLFORD L, BENNETT M D, SIMS C, THOMAS N, FRIEND J A, NICHOLLS P K, WARREN K S & O'HARA A J 2009. prevalence, emergence, and factors associated with a viral papillomatosis and carcinomatosis syndrome in wild, reintroduced, and captive western barred bandicoots (*Perameles bougainville*). *EcoHealth* 6, 414–425.
- Wooller R D, Renfree M B, Russell E M, Dunning A, Green S W & Duncan P 1981. Seasonal changes in a population of nectar feeding marsupial *Tarsipes spencerae* (Marsupialia, Tarsipedidae). *Journal of Zoology* 195, 267–279.
- WOOLLEY P A 1977. In search of the Dibbler, Antechinus apicalis (Marsupialia: Dasyuridae). Journal of the Royal Society of Western Australia 59, 111–118.

- Woolley P A 1980. Further searches for the Dibbler, Antechinus apicalis (Marsupialia: Dasyuridae). Journal of the Royal Society of Western Australia 63, 47–52.
- Woolley P A 1991. Reproductive pattern of captive Boullanger Island dibblers, *Parantechinus apicalis* (Marsupialia: Dasyuridae). *Wildlife Research* 18, 157–163.
- WOOLLEY P A 2008a. Brush-tailed Mulgara, Dasycercus blythi (Waite, 1904). In: Van Dyck S & Strahan R (eds) The Mannuals of Australia, pp. 47–48. Reed Holland Publishers, Sydney.
- Woolley P A 2008b. Butler's dunnart, Sminthopsis butleri (Archer, 1979). In: Van Dyck S & Strahan R (eds) The Manimals of Australia, pp. 130–131. Reed Holland Publishers, Sydney.
- Woolley P A 2008c. Dibbler, *Parantechinus apicalis* (Gray, 1842). *In*: Van Dyck S & Strahan R (eds) *The Manimals of Australia*, pp. 65–66. Reed Holland Publishers, Sydney.
- Woolley P A 2008d. Fat-tailed pseudantechinus, *Pseudantechinus macdonnelleusis* (Spencer, 1895). *In*: Van Dyck S & Strahan R (eds) *The Manunals of Australia*, pp. 69–70. Reed Holland Publishers, Sydney.
- WOOLLEY P A 2008e. Kaluta, Dasykaluta rosamondae (Ride, 1964).
 In: Van Dyck S & Strahan R (eds) The Mammals of Australia,
 pp. 51–52. Reed Holland Publishers, Sydney.
- Woolley P A 2008f. Ningbing pseudantechius, *Pseudantechinus ningbing* (Kitchener, 1988). *In*: Van Dyck S & Strahan R (eds) *The Mammals of Australia*, pp. 73–74. Reed Holland Publishers, Sydney.
- Woolley P A 2008g. Red-cheeked Dunnart, Sminthopsis virginiae (Tarragon, 1874). In: Van Dyck S & Strahan R (eds) The

- Manumals of Australia, pp. 158–159. Reed Holland Publishers, Sydney.
- Woolley P A 2008h. Woolley's pseudantechius, *Pseudantechinus* woolleyae (Kitchener and Caputi, 1988). *In:* Van Dyck S & Strahan R (eds) *The Mammals of Australia*, pp. 76–77. Reed Holland Publishers, Sydney.
- WRIGHT L J, SMITH J A & RICHARDSON J 2007. BiblioRingtailPossum: the western ringtail possum, Pseudocheirus occidentalis (Thomas, 1888), a subject-specific bibliography. Conservation Science Western Australia 6, 159– 176.
- Yadav M 1971. The transmission of antibodies across the gut of pouch young marsupials. *Immunology* 21, 839–851.
- Yadav M, Stanley N F & Waring H 1972. The thymus glands of a marsupial, Setonix brachyurus (quokka), and their role in immune responses. Structure and growth of the thymus glands. Australian Journal of Experimental Biology and Medical Science 50, 347–356.
- Zosky G R & Larcombe A N 2003. The parasympathetic nervous system and its influence on heart rate in torpid western pygmy possums, *Cercatetus concinnus* (Marsupialia: Burramyidae). *Zoology* **106**, 143–150.
- ZOSKY G R & O'SHEA J E 2003. The cardiac innervation of a marsupial heterotherm, the fat-tailed dunnart (*Sminthopsis crassicaudata*). *Journal of Comparative Physiology B* 173, 293–300.

Received 17 May 2013; accepted 21 August 2013

Australia.	
Western	
Marsupials of V	
ppendix 1	

Taxa	Common names	Body mass	Habitat	Status	Reference
Dasyuridae Antechinus flavipes (A. f leucogaster ^{End})	Yellow-footed antechinus, mardo	26-79 g males 21-52 g females	Varied habitats from forests to swamps and dry mulga country.		Crowther 2008
Dasycercus blythi	Brush-tailed mulgara	75-110 g males 60-90 g females	Constructs burrows in sandy swales in spinifex grassland; medium to dense cover.	P4	Woolley 2008a
Dasycercus cristicanda	Crest-tailed mulgara, ampurta	110-185 g males 65-120 g females	Constructs burrows in desert sand dunes with sparse cover.	V, S1[v]	Masters 2008
Dasykaluta rosanıondae ^{End}	Kaluta	25-40 g males 20-30 g females	Hummock grasslands of the Pilbara.		Woolley 2008e
Dasyurus geoffroii	Western quoll, chuditch	mean 1310 g males mean 890 g females	Sclerophyll forest, dry woodland or shrubland of the south-west WA.	V, S1[v]	Serena & Soderquist 2008
Dasyurus hallucatus	Northern quoll	340-1120 g males 240-690 g females	Most commorily rocky escarpments; also woodlands.	E, S1[e]	Oakwood 2008
Ningani ridei	Wongai ningaui	6.5-10.5 g	Inland red sandplains supporting spinifex hummock grassland.		McKenzie & Dickman 2008
Ningaui timealeyi ^{End}	Pilbara ningaui	3.6-9.5 g males 3.5-7.5 g females	Along drainage lines in spinifex grasslands of the Pilbara.		Dunlop et al. 2008
Ningani yvonnae	Southern ningaui, mallee ningaui	6-14 g	Spinifex grasslands Great Victoria Desert.		Carthew & Bos 2008
Parantechinus apicalis End	Dibbler	60-125 g males 40-73 g females	Coastal and subcoastal areas.	E, S1[e]	Woolley 2008c
Phascogale calura	Red-tailed phascogale, red-tailed wambenger	39-68 g males 38-48 g females	Isolated patches of forest in the south-west.	E, S1[e]	Bradley et al. 2008
Phascogale tapoatafa	Brush-tailed phascogale, common wambenger	175-311 g males 106-212 g females	Arboreal specialist, open forest with sparse groundcover.	S1[v]	Soderquist & Rhind 2008
Antechinomys laniger	Kultarr, jerboa marsupial mouse	mean 30 g males mean 20 g females	Desert plains, grasslands and acacia woodland.		Valente 2008
Planigale ingrami	Long-tailed planigale	2.8-6.6 g males 2.6-5.8 g females	Blacksoil plains of the tropical north.		Fisher 2008
Planigale maculata	Common planigale	4-16.3 g males 3.5-17.2 g females	Coastal and subcoastal areas of north-west.		Burnett 2008
Pseudantechinus macdonnellensis	Fat-tailed pseudantechinus	25-45 g males 20-40 g females	Rocky hills, breakaways, red sandplains of northern deserts.		Woolley 2008d
Pseudantechinus ningbing	Ningbing false antechinus	20-25 g males 15-20 g females	Limestone and sandstone outcrops of the Kimberley.		Woolley 2008f
Pseudantechinus roryi ^{End}	Rory's pseudantechinus	19-32 g males 17-26 g females	Open woodland, spinifex sandplain, granite rockpiles of the Pilbara.		Cooper 2008
Pseudantechinus woolleyae End	Woolley's pseudantechinus	35-50 g males 30-45 g females	Rocky habitats through Pilbara and western deserts.		Woolley 2008h

Taxa	Common names	Body mass	Habitat	Status	Reference
Sminthopsis butleri	Butler's dunnart	15-30 g	Open tropical woodland on blacksoil/sand; Kulumbaru WA and Tiwi Islands NT	V, S1[v]	Woolley 2008b
Sminthopsis crassicandata	Fat-tailed dunnart	$10-20~\mathrm{g}$	Varied habitats across the southern half of the continent.		Morton & Dickman 2008a
Sminthopsis dolichura	Little long-tailed dunnart	11-20 g males 10-21 g females	Semi-arid and arid south-western WA and SA.		Friend & Pearson 2008
Sminflopsis gilberti ^{End}	Gilbert's dunnart	14-25 g	Woodlands of the Darling Scarp, mallee-heaths in the central and southern wheatbelt.		Morris & McKenzie 2008
Sminthopsis granulipes ^{End}	White-tailed dunnart	18-37 g	Proteaceous shrublands of semi-arid regions of south-west WA.		McKenzie & Kitchener 2008
Sminthopsis griseoventer	Grey-bellied dunnart	15-24 g males 14-20 g females	Coastal plain and lateritic ranges of south-west WA.		Dickman 2008
Sminthopsis hirtipes	Hairy-footed dunnart	13-19.5 g	Open low woodlands or spinifex grasslands of south-central red sandplains		Pearson & McKenzie 2008
Sminthopsis longicandata	Long-tailed dunnart	15-25 g	Arid, rocky country through the Pilbara, Gibson i Desert to Alice Springs.	P4	Burbidge, et al. 2008d
Sminthopsis macroura	Stripe-faced dunnart	15-25 g	Widely through arid and semi-arid Australia, particularly shrubland and tussock grasslands.		Morton & Dickman 2008b
Sminthopsis ooldea	Ooldea dunnart	9-17 g males 8-15 g females	Primary mulga shrublands and woodlands with tussock understory, through the Pilbara and central continent.		Foulkes 2008
Sminthopsis psanmophila	Sandhill dunnart	26-55 g males 25-42 g females	Tussock grasslands, low open woodland; isolated populations in the Great Victoria Desert.	E, S1[e]	Pearson & Churchill 2008
Sminthopsis virginiae	Red-cheeked dunnart	31-58 g males 18-34 g females	Tropical savannah woodlands; isolated populations in the Kimberley.		Woolley 2008g
Sminthopsis youngsoni	Lesser hairy-footed dunnart	8.5-12.0 g	Open shrublands of hummock grassslands through Pilbara and central Australia.		McKenzie & Cole 2008
Myrmecobiidae Myrnecobius fasciatus	Numbat, banded anteater	405-752 g males 305-647 g females	Open woodlands with abundant termite activity.	V, S1[v]	Friend 2008b
Peramelidae Chaeropus ecandatus	Pig-footed bandicoot	200 g (estimated)	Sand dunes and sandplains with hummock grassland and tussock grass.	Ex, S2	Johnson & Burbidge 2008a
Isoodon auratus (I. a. auratus; mainland) (I. a. barrowensis ^{End} : Barrow Island)	Golden bandicoot	300-670 g (l. a. auratus) 250-600 g (l. a. barrowensis)	Sandplain or sand-dune spinifex grasslands.	V, SI[v]	McKenzie et al. 2008
Isoodon macronrus	Northern brown bandicoot	500-3100 g males 500-1700 g females	Varied habitats through tropical north and eastern states.		Gordon 2008b

Isoodon obesulus (I. o. fusciventer ^{End} ; Western Australia)	Southern brown bandicoot, quenda	500-1850 g males 400-1200 g females	Forest, woodland, shrub and heath communities.	P5	Paull 2008
Perametes bougainville (P. b. bougainville; Shark Bay) (P. b. myosuros; mainland Western Australia)	Western barred bandicoot	168-280 g males 165-379 g females	Dense scrub, low heath or hummock grasslands.	E, S1[e] (P. b. bongainville) Ex (P. b. myosuros)	Friend 2008c
Perameles eremiana	Desert bandicoot	unknown	Sandplain and sand-ridge desert with spinifex grassland.	Ex, S2	Gordon 2008a
Thylacomyidae Macrotis lagotis	Bilby, rabbit-eared bandicoot	1000-2500 g males 800-1100 g females	Desert sandplains and dunes fields, hummock	V, S1[v]	Johnson 2008a
Macrotis lencura	Lesser bilby	360-435 g males 311 g female	Gibson desert.	Ex, S2	Johnson 2008b
Notoryctidae					
Notoryctes caurinus End	Northern marsupial mole, kakarratul	30-50 g	Sand-dune deserts of north-western Australia.	E, S1[e]	Benshemesh & Aplin 2008
Notoryctes typhlops	Southern marsupial mole, itjaritjari	40-70 g	Sand-dune deserts of central Australia.	E, S1 [e]	Benshemesh 2008
Vombatidae					
Lasiorlinus latifrous	Southern hairy-nosed wombat	19-36 kg males 17.5-36 kg females	Semi-arid grasslands of southern Australia.		Taggart & Templesmith 2008
Burramyidae					
Cercartetus concinnus	Western pygmy possum	8-21 g	Mallee woodlands, heathlands, shrubland and dry sclerophyll of southern Australia.		Carthew et al. 2008
Tarsipedidae					
Tarsipes rostratus ^{End}	Honey possum	7-11 g males 8-16 g females	Coastal sandplain heaths with abundant nectar- producing Proteaceae and Myrtaceae.		Renfree 2008
Petauridae					
Petaurus breviceps	Sugar glider	115-160 g males 95-135 g females	Forest containing tree hollows and varied food sources.		Suckling 2008
Pseudocheiridae					
Petropseudes dahli	Rock ringtail possum	1280-2000 g	Rocky outcrops of the Kimberley and tropical northern Australia.	P3	Webb et al. 2008
Pseudocheirus occidentalis End	Western ringtail possum	700-1300 g males 750-1200 g females	Jarrah, wandoo, marri and especially coastal peppermint forest and woodland.	V, S1[v]	de Tores 2008b
Phalangeridae					
Trichosurus vulpecula	Common brushtail possum	1300-4500 g males 1200-3500 g females	Varied, though prefers dry eucalypt forests and woodlands.		Kerle & How 2008
Wyulda squamicaudata End	Scaly-tailed possum	900-2000 g	Open woodland and closed forests of the rugged, rocky country of the Kimberley.	P3	Burbidge & Webb 2008

Taxa	Common names	Body mass	Habitat	Status	Reference
Potoroidae					
Bettongia lesueur	Burrowing bettong	mean 680 g	Coastal heath with limestone cap-rock, though formerly more widespread.	V, S1[v]	Burbidge & Short 2008
Bettongia penicillata (B. p. olgibyi; Western Australia)	Woylie	980-1850 g males 750-1500 g females	Wheatbelt thickets containing Gastrolobium spp.; historically broad arid and semiarid distribution.	E, S1[e]	de Tores & Start 2008
Bettongia pusilla	Nullarbor dwarf bettong			Ex, S2	Burbidge 2008a
Potorous gilbertii ^{End}	Gilbert's potoroo	845-1200 g males 708-1205 g females	Melaleuca heath with dense sedge understory or adjacent closed woodland.	CE, \$1[ce]	Friend 2008a
Potorous platyops	Broad-faced potoroo	unknown	Unknown.	Ex, S2	Kitchener & Friend 2000
Macropodidae					
Lagorchestes asomatus	Central hare-wallaby	unknown; similar to burrowing bettong	Arid sandplains and dunes of Gibson Desert and surrounding areas.	Ex, S2	Burbidge et al. 2008b
Lagorchestes conspicillatus (L. c. conspicillatus; Barrow Island)	Spectacled hare-wallaby	1600-4750 g	· Tropical grasslands and open shrublands.	V, S1[v] (L. c. conspicillatus) P3 (L. c. leichardti)	Burbidge & Johnson 2008
(L. c. leichardti; mainland)					
Lagorchestes hirsutus (L. h. bernieri ^{End.} ; Bernier and Dorre Islands) (L. lt. NTM U2430; mainland)	Rufous hare-wallaby, mala	mean 1580 g males mean 1740 g females (L. ll. bernieri); mean 1220 g males mean 1310 g females (L. ll. NTM U2430)	Spinifex hummock, tussock grasslands and shrublands of arid and semi-arid areas.	E, S1[e] (<i>L. h. NTM U2430</i>) V, S1[v] (<i>L. h. bernieri</i>) Ex SW mainland	Johnson & Burbidge 2008b
Macropus agilis	Agile wallaby	16-27 kg males 9-15 kg females	Riperian vegitation in open forest and adjacent grasslands of the tropic north.		Merchant 2008
Macropus antilopinus	Antilopine kangaroo	18.6-51 kg males 14-24.5 kg females	Scattered to dense vegetation with grass-dominated understory of monsoonal tropical woodlands.	Ritchie 2008	
Macropus eugenii (М. e. derbianus ^{End} ; Western Australia)	Tammar wallaby	6-10 kg males 4-6 kg females	Dense low scrub with adjacent grassy areas for feeding.	P5	Hinds 2008
Macropus fuliginosus	Western grey kangaroo	18-72 kg males 17-39 kg females	Varied habitats across southern Australia; consumes principally graze but also some browse.		Coulson 2008
Macropus irma ^{End}	Western brush wallaby, black gloved wallaby	7-9 kg	Open forest or woodland with low grass and open thickets.	P4	Morris & Christensen 2008
Macropus robustus (M. r. erubescens; mainland) (M. r. isabellinus End; Barrow Island) (M. r. woodwardi; mainland	Euro, common wallaroo	7.25-60 kg males 6.25-28 kg females	Varied habitats across arid, semi-arid and tropical Australia usually containing steep escarpments or rocky hills.	V, SI[v] (M. r. isabellinus)	Clancy & Croft 2008
Vimboulory					

Croft & Clancy 2008	Burbidge 2008b Ingleby & Gordon 2008	Eldridge & Telfer 2008	Pearson et al. 2008	Sanson & Churchill 2008	Eldridge & Pearson 2008	Pearson & Eldridge 2008	de Tores 2008a	Prince & Richards 2008
	Ex, S2		P4		V, S1[v]		V, S1[v]	Ex (L. f. albipilis) V, S1[v] (L. f. fasciatus)
Open plains of arid and semi-arid Australia.	Varied habitats in arid and semi-arid Australia. Open woodlands with tussock grass or grasslands with scattered trees or shrubs of northern Australia.	Rocky hills, gorges and escarpments with savannah woodland in the Kimberley and NT.	Low open woodland and vine thickets with rocky outcrops.	Varied vegetation including floodplain, vine thickets, rainforest, and grassland with rocky shelter.	Varied and discontinuous rocky habitats.	Rocky environments with surrounding spinifex grasslands and shrublands of the Pilbara and Ashburton regions.	Shrub thickets and sedges on Rottnest Island; riparian vegetation.	Dense thickets of Acacia spp.
22-92 kg males 17-39 kg females	~3.5 kg 6-9 kg males 4.5-7 kg females	3.2-5.6 kg males 2.2-4.7 kg females	960-1430 g	1050-1500 g males 1070-1700 g females	4.1-5.3 kg males 3.1-3.8 kg females	3.7-6.6 kg mainland 2.6-3.9 kg Dampier Archipelago	2.7-4.2 kg males 1.6-3.5 kg females	1.0-2.3 kg
Red kangaroo	Crescent nail-tail wallaby Northern nail-tail wallaby	Short-eared rock-wallaby	Monjon	Nabarlek, little rock wallaby	Black-flanked rock-wallaby, Black-footed rock-wallaby	Rothschild's rock-wallaby	Quokka	Banded hare-wallaby, merrnine
Macropus rufus	Onychogalea lunata ^{End} Onychogalea unguifera	Petrogale brachyoti	Petrogale burbidgei ^{End}	Petrogale concinna	Petrogale lateralis (P. I. ANWC CM15314 End.; MacDonnell Ranges) (P. I. hacketti; south coast islands) (P. I. lateralis; mainland) (P. I. lateralis; mainland) (P. I. WAM M15135 E; West Kimberley)	Petrogale rotlischildi ^{End}	Setonix brachyurus ^{End}	Lagostrophus fasciatus (L. f. albipilis; mainland) (L. f. fasciatus ^{Ens.} ; Bernier and Dorre Islands)

End indicates taxa endemic to Western Australia.

Environment Protection and Biodiversity Conservation Act 1999 status codes:

Ex, extinct (taxa not definitely located in the wild during the past 50 years)

CE, critically endangered (taxa facing an extremely high risk of extinction in the wild in the immediate future

E, endangered (taxa facing a very high risk of extinction in the wild in the near future)

V, vulnerable (taxa facing a high risk of extinction in the wild in the medium-term future) Western Australian Wildlife Conservation Act 1950 status codes: S2, Schedule 2 (fauna that is presumed to be extinct)

51, Schedule 1 (threatened fauna; fauna that is rare or is likely to become extinct) with rankings shown in square parentheses: [ce], critically endangered; [e], endangered; [v], vulnerable.

Western Australian Department of Environment and Conservation (DEC) priority species status codes:

P2, Priority 2 (poorly known species on conservation lands) P1, Priority 1 (poorly known species on threatened lands)

P3, Priority 3 (poorly known species, some on conservation lands)
P4, Priority 4 (rare, near threatened and other species in need of monitoring)
P5, Priority 5 (conservation dependent species)



Chemical fingerprinting of gold using laser ablation-inductively coupled plasma-mass spectrometry (LA-ICP-MS)

R J WATLING 1*, C J SCADDING 2 & C D MAY 2

- ¹ Centre for Forensic Science, University of Western Australia, 35 Stirling Highway, Crawley, WA 6009, Australia.
- ² TSW Analytical Pty Ltd, 2/27 Clark Court, Bibra Lake, WA 6163, Australia.
- * Corresponding author 🖾 john.watling@uwa.edu.au

Internationally, ~2500 t of gold is produced annually in mining operations covering over 60 countries. South Africa produces ~290 t, Australia and the USA ~260 t each and China ~220 t. Quite naturally very few accurate figures for gold theft internationally are available. However, South African sources estimate that some 35 t of gold were stolen annually from mines and refineries during the period 1994–1998, an amount representing over \$1.5 billion per annum. Because gold is essentially untraceable, it is considered the ideal illicit international currency. The requirement to identify the source of stolen gold has resulted in the development of a gold fingerprinting protocol, using laser ablation–inductively coupled plasma–mass spectrometry (LA-ICP-MS), the use of which has significantly increased over the last 20 years. This paper overviews the development and application of the technology and highlights its use in specific cases of gold theft.

KEYWORDS: chemical fingerprinting, gold theft, LA-ICP-MS.

INTRODUCTION AND BACKGROUND TO THE ILLICIT TRADE IN GOLD

Gold has always held a fascination for mankind; it is one of the very few coloured metals that occur naturally, another being copper, which was the basis of the Bronze Age culture of the Western World. Gold is often considered the ultimate indication of an individual's wealth and over the centuries has been traded and stolen and more recently used as 'ghost currency' in the illicit international trade in both weapons and drugs. Today, with almost all of the world's alluvial deposits either discovered or worked out, it is necessary to mine gold from host rocks that can contain as little as one part per million of the metal, in initiatives from openpits to deep underground workings. Pre-concentration and preliminary refining of the metal on site, often in remote areas, increases the possibility of illicit removal and trade in the metal and today it is estimated that considerably in excess of \$US2 billion is stolen annually at source from the world's mines and refineries making gold a significant source of income for major crime syndicates. Gold production, annually lost to theft in such countries as South Africa (Coetzee & Horn 2007), makes up for a large percentage of the total production value (Gastrow 2001). The domino effect of job loss leading to a variety of economical and social problems (impoverishment is one of the largest causes of the high crime rate in South Africa) has crippling effects on entire communities in South Africa and compounding the urgency to develop protocols to identify, recover and ultimately stop theft and illicit trade in the metal.

The illegal trade in stolen precious metals is extremely profitable due to their high values and established identities as global currencies. The ultimate beneficiaries of this illegal trade are normally well-organised bodies that are also involved in a variety of other illegal activities, such as drugs and firearms smuggling. These

organisations present a global threat, and should be monitored and opposed on an international level. Established money-laundering systems using gold have been found in many European countries, such as Switzerland and Italy, and from there across the world, including the USA, and South and Central America (Reuter & Truman 2004; Masciandaro 2004; Zdanowicz 2004; Woolner 1994; Baere & Schneider 1990; Lilley 2003; Grosse 2001).

Reportedly, Uruguay became the leading gold supplier to the USA during 1989 even though the country had no gold industry (Williams 1997; Zeldin 1997; Millard 1999). The gold 'trade' was simply a front for laundering profits made in the illegal narcotics trade (Levi & Reuter 2006). International terrorist groups also regularly use gold as a bargaining tool. Prior to and during the US attack on Afghanistan, Al-Qaeda moved large funds out of the country by smuggling gold, diamonds and other precious stones across the borders, and then to Dubai from where the funds were spread across the world, including the USA (Shehu 1997; El Qorchi et al. 2003; Warde 2007). Due to the general absence of formal banking systems in the Middle East, North Africa and Asia the informal Hawala system is often used to refund gold deliveries, where money is transferred across large distances by email or telephone calls, and all records destroyed afterward (Abuza 2003; de Goede 2003; Jamwal 2002). These and many other routes exist whereby illegal funds can be legitimised, using precious metals and precious stones, often themselves having been obtained by illegal means.

It is the involvement of organised crime syndicates that makes policing the theft of gold extremely difficult as informants, willing to risk their own and their family's lives, are hard to find. Consequently it is necessary to establish a mechanism that can be used to trace recovered gold back to its source and direct scarce police and security activity specifically to that source. While increasing security at all mine sites to detect and stop theft may not

be a commercially sensible measure, if it is possible to retrospectively establish the provenance of recovered gold it is then possible to target specific mine sites and introduce more rigorous control and monitoring of mine personnel to ultimately reduce the theft of the metal.

Trace-element fingerprinting of gold-containing materials is a technique aimed at the determination and quantification of minor and trace components. The technique allows the unique characterisation of materials as they pass from ores and precious-metal minerals to flotation concentrates, smelter products, and variously refined products. The use of specially designed statistical software allows allocation of individual analyses to material groups and performs a comparison and allocation of probabilities for the similarity to other data in the database (Watling *et al.* 1993).

In geology, understanding the compositional fingerprints should permit the identification of genetic processes, based on the assumption that differences or changes in the ore-forming processes (e.g. intrinsic conditions of hydrothermal fluids or magmas) will be reflected in the trace-element pattern of ore minerals (or of associated minerals which inevitably are also introduced into the beneficiation process). In forensic science, identifying the original source of precious-metal materials recovered during police operations is of huge financial interest. Although crime statistics are incomplete (it is estimated that only 1.4–2.8% of all stolen gold is recovered), indications are that between 0.8 and 1.6% of the world gold production gets stolen annually in South Africa alone (\$250-500 million) with an additional \$20-50 million stolen in Australia (Coetzee & Horn 2011; Walker 1997; Walker & Unger 2009).

Initial research to identify a method for goldprovenance establishment led to the development of the technique of gold spectral-fingerprinting (Watling et al. 1993). This technique is based on the premise that gold, associated with a specific mineralising event (an event in geological time, sometimes lasting many millions of years) or extractive process, will inherit a trace-/ultra-traceelement signature unique to that event or process. Native gold is a mineral composed mainly of Au, Ag and Cu in solid solution and contains trace metals as lattice impurities, mineral inclusions, at and along grain boundaries or in surface coatings. The combination of Au, Ag and Cu as primary indicators, together with as wide a range of trace and minor analytes as possible, provides an elemental and isotopic fingerprint or profile which can uniquely identify a deposit or source of the gold. The uniqueness of this metal assemblage facilitates provenance establishment of the gold in question. However, the fingerprint of refined gold may be significantly different to that of natural unprocessed gold obtained from the same ore, although certain elements will remain throughout refining procedures, albeit at much reduced levels, thereby enabling comparison back to the original material and from there potentially to the mine of origin.

ANALYTICAL TECHNIQUE

The analytical technique of choice in gold-provenance establishment is laser ablation-inductively coupled plasma-mass spectrometry (LA-ICP-MS). Research

detailed in this paper was primarily undertaken using an Agilent 7500CS High sensitivity ICP-MS and a New Wave UP213 laser ablation system. This technique has been used successfully to identify elemental association patterns (spectral fingerprint) of processed gold, gold ores and jewelry recovered in police operations in Australia, South Africa, Indonesia, New Zealand, England, Japan, America and Scandinavia. By comparison of elemental association patterns it has been possible to relate processed and unrefined gold back to individual refined batches and mines of origin. LA-ICP-MS (Watling et al. 1994) has now been used successfully to obtain the inter-element association pattern, 'fingerprint' of gold in forensic investigations internationally (Freeman et al. 1994; Kogan et al. 1994; Watling 1996; Watling et al. 1997), for fingerprinting scene of crime evidence (Herbert & Watling 1997; Watling 1999; Watling et al. 1995) and as a provenance-sourcing tool (Outridge et al. 1998; Sie et al. 1996; Taylor et al. 1997). Because the analytical detection limits are so low, a large number of inter-element association patterns can be employed to develop unique trace-/ultra-trace-element associations in gold. Commonly, elemental data are obtained for over 50 elements. Consequently, the number of elements that can usefully be employed to provide data to establish the fingerprint is extremely large thus increasing the robustness of the spectral fingerprint as a provenance establishment tool. Each ablation event consumes only a fraction of a microgram of sample and it is usually possible to retain a significant proportion of the sample for subsequent further forensic examination and corroborative analyses. In addition, samples can also be stored in a physical database for reference into the future. This aspect has considerable appeal as, in any forensic investigation, it is preferable to retain some of the original sample for corroborative analysis. However, a significant problem with LA-ICP-MS is that the analytical area is extremely small (between 20 and 100 µm) and that the coupling efficiency of the laser will vary from sample to sample. The effect of a small sample area is that, if the sample is inhomogeneous, analytical data may vary from analytical site to analytical site. To overcome this, multiple analyses (usually at least 10) are performed on each sample to obtain a representative picture of the spectral fingerprint of the gold being analysed. The fact that coupling efficiency cannot be controlled means that, under a lasing regime where there is high coupling efficiency, more sample will be removed to the analytical plasma than under conditions where there is lower coupling efficiency. Under these conditions analytical sensitivity will vary between sample sites but inter-element ratios will not, and this comparison of inter-element relationships is the basis of gold fingerprinting.

An issue that hinders the widespread use of LA-ICP-MS in forensic science is the shortage of appropriate solid certified reference materials and solid standards in general. Without standards quantitative data and method validation are impossible to achieve. In fact quantitative analysis is a serious problem for LA-ICP-MS because although relative measurements are sufficient in many cases, ultimately where data use in court is required, absolute concentration measurements will become more and more necessary. However, the use of relative interelement association patterns is perfectly acceptable for provenance establishment purposes.

Instrument response optimisation

National Institute of Standards and Technology Standards (NIST) Glasses, SRM610 and SRM612 are used to optimise the instrument operating parameters. In addition, the use of these standards at the beginning and end of a complete analytical protocol allow quantification of changes in mass response with time to be made. This procedure also facilitates inter-comparison and normalisation of data on a day to day basis. The choice of these samples and not gold is governed by the fact that optimisation requires a steady-state signal and no laser ablation standards for gold exist. The fact that glass and gold are dissimilar sample types, and that plasma loading will be different for the two matrices, is not relevant as the interpretational protocol for fingerprinting is based on the inter-element association pattern of samples and not on absolute analyte quantitation. The use of NIST standards has proved to be robust and extremely convenient. Once optimisation has been achieved, it is necessary to analyse a series of in-house matrix standards to provide a cross-reference to previously obtained data. In practice, three fabricated gold blocks, each weighing approximately 50 g, are analysed either every 10 study samples or a minimum of three times during any specific sample batch. These inhouse gold standards were prepared by combining residual gold from a number of case studies. The molten gold was quenched in chilled water to ensure minimal analyte segregation. The actual element mixture and concentration are immaterial as the standards are used simply to ensure correspondence of day to day and ultimately, long-term analytical data. These samples have been used for the last 12 years for this purpose and the data therefore provide a continuous ability to cross reference on a year to year basis and even to crossvalidate methodology when changing both laser and ICP instrumentation.

Analytical procedure

Prior to analysis all samples are individually ultrasonicated for 5 minutes in a mixture of 50% ethanol and 50% water to remove all adhering debris. Where the

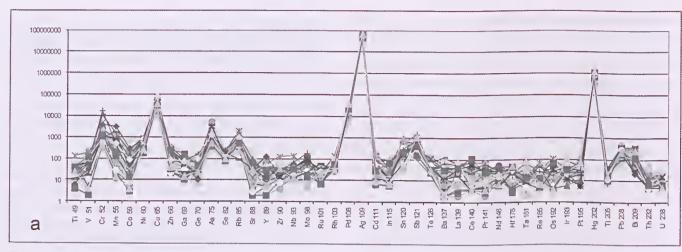
size of the sample is extremely small, this stage may be omitted and simple reference made to the time/intensity graphs of the individual elements made to establish if surface contamination exists. Under these circumstances a significant peak for such analytes as sodium, aluminum and iron will occur immediately after the first laser pulse and the signal will quickly return to a plateau, representing the bulk analyte concentration of the sample, once the surface contamination has been removed. Ignoring this initial peak can be easily achieved when the time/response curves are inspected. The analytical signal can then simply be integrated after this initial peak thus removing the influence of surface contamination in the overall analysis. Where possible, at least five sites on each gold sample are analysed using the continuous data acquisition facility of the ICP-MS software. This facility allows the operator to view time slices of the data and select individual areas for analytical comparison. Selection of appropriate areas is based on relative uniformity of signal during the analytical event and implies that the areas of the gold being sampled are free from inclusions and more appropriately represent the bulk composition of the gold. The selected areas of all scans are then combined and response counts per second calculated for each element isotope for ultimate comparison using conventional statistical approaches. This aspect is particularly important when establishing the spectral fingerprint of gold as this material can contain exsolved inclusions of extremely wide analytical complexity and it is necessary to have knowledge of the mineralogy and heterogeneity of the samples prior to interpretation. Prolonged laser ablation can often penetrate these zones and give rise to variations in the elemental response pattern. Often variations in elemental concentrations occur associated with regrowth episodes during the emplacement of the gold and can be identified by relating the elemental scan response function to specific areas on the sample.

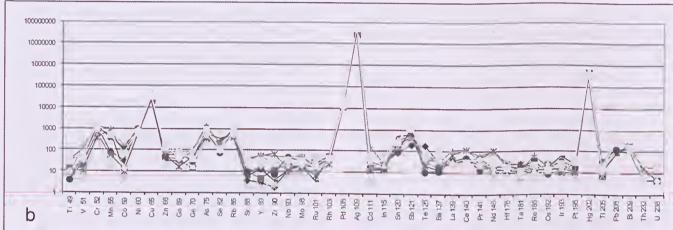
Sample analysis

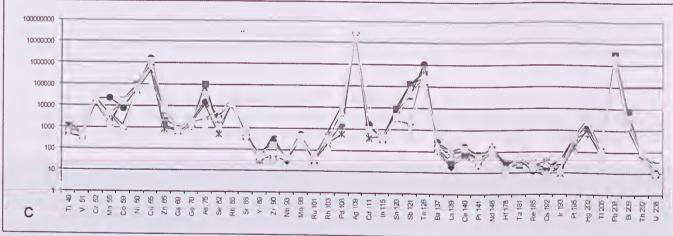
Samples are usually mounted for analysis on 25 mm diameter, 3–4 mm thick square Perspex blocks (Figure 1)

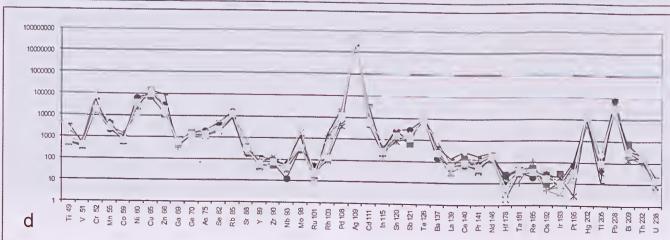


Figure 1 Gold samples mounted for analysis using LA-ICP-MS. (Ideally each block contains at least three replicates of each sample and each block can hold up to eight samples).









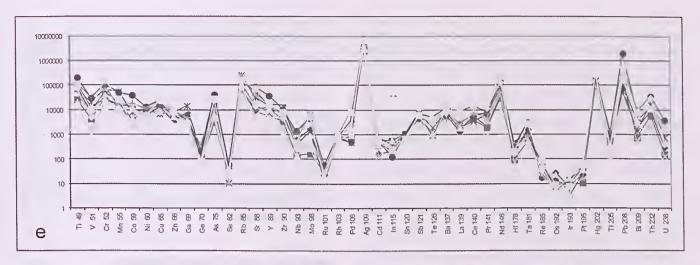


Figure 2 (a) Reproducibility of spectral fingerprint of all samples of stolen gold; (b) of gold from Reference Mine A; (c) of gold from Reference Mine B; (d) of gold from Reference Mine C; (e) of gold from Reference Mine D.

using cyanoacrylate glue as many of the samples received are small (<1 mm³) and even large samples are usually subsampled before analysis. Sample blocks are usually labelled on the back with a reference number (D, E and F in Figure 1) with a blue mark in the upper left hand corner of the upper surface to orient the sample mount under the laser. Samples are then analysed sequentially from the top left to bottom right. A blue colour is used because it is easily identified from any other material on the sample mount.

Ablation is undertaken for ~120 seconds. Data are recorded using a time/response graph where the counts per second data for all analytes are essentially simultaneously recorded with reference to the time postinitiation of lasing. This procedure allows the graph to be inspected retrospectively and when an inclusion of an obviously contaminating ore or gangue mineral has been ablated the analytical data for this time interval is easily apparent and can be retrospectively removed before final counts per second data are computed. The isotopes 45Sc, ⁴⁸Ti, ⁵¹V, ⁵²Cr, ⁵⁵Mn, ⁵⁹Co, ⁶⁰Ni, ⁶⁵Cu, ⁶⁶Zn, ⁷¹Ga, ⁷³Ge, ⁷⁵As, ⁸²Se, ⁸⁵Rb, ⁸⁸Sr, ⁸⁹Y, ⁹⁰Zr, ⁹³Nb, ⁹⁸Mo, ¹⁰²Ru, ¹⁰³Rh, ¹⁰⁸Pd, ¹¹¹Cd, ¹¹⁵In, ¹²⁰Sn, ¹²³Sb, ¹²⁶Te, ¹³³Cs, ¹³⁸Ba, ¹³⁹La, ¹⁴⁰Ce, ¹⁴¹Pr, 146Nd, 151Eu, 152Sm, 158Gd, 159Tb, 162Dy, 165Ho, 166Er, 169Tm, 172Yb, 175Lu, 178Hf, 181Ta, 182W, 187Re, 192Os, 193Ir, 195Pt, 202Hg, ²⁰⁵Tl, ²⁰⁸Pb, ²⁰⁹Bi, ²³²Th and ²³⁸U are usually used for gold characterisation. In some cases, however, where an element is present below or close to the detection limit of the technique, it is removed from the data prior to data interpretation.

INTERPRETATION PRINCIPLE

Interpretation of the mass-spectral data, obtained using the protocols described, may be subdivided into the following activities: (i) direct comparison of the raw spectral data; (ii) comparison of the raw count data using comparability statistics; (iii) inter-element association plots; (iv) comparison of data using principal component analysis; and (v) comparison of data using linear discriminant analysis.

Direct comparison of the raw spectral data

Comparison of the inter-element association pattern (fingerprint) is the initial screening test to establish if there are general similarities or differences between the individual spectra under investigation. It could therefore logically be anticipated that inter-element association patterns would be different if gold originated from different mineralising events. Consequently, the confirmation that their fingerprints are different may be considered as a 'proof' of a geologically identifiable observation. The vertical scale on these spectra, which is an approximation of the relative concentration of the abundance of each isotope in the sample, is given on the ordinate. Providing that the spectra are graphically presented on comparable abscissa and ordinate scales, visual comparison is valid to distinguish between both similar and significantly different gold samples. This type of comparison requires significant skill and experience and is often time consuming when a large number of samples have to be compared. Consequently it is useful to sort the spectra into comparable blocks in order to minimise time and assist in the interpretation process.

Comparison of raw count data

Visual comparison of spectral data is frequently demanding with similarities and differences between the actual spectra being difficult to discern and quantify by both trained and untrained personnel. Consequently, comparison of raw count data for selected analytes is often preferred as a simple means of displaying data. This can be achieved extremely quickly using a computerised search/match statistical routine known as a comparability index. The comparability index statistics are based around a sorting subroutine that identifies the logarithmic values of the raw count data and compares these with equivalent element values in the remaining database samples. These differences are then summed and sorted to obtain an approximation of the comparability of the spectra. The series is sorted on the basis of the difference from a 100% fit of the questioned

sample with itself. A 100% fit can only be achieved with absolutely identical spectra being compared, a situation which will never exist in a chemical analysis and is only possible by duplicating the questioned sample in the database. The 100% fit ensures that the maximum possible comparability point is fixed in the interpretational protocol. The worse fit of the questioned sample to one of the other samples in the database is given a 0% comparability rating. Obviously both the top and the bottom database fit are artificial. However, the comparability mathematical routine is only designed to rank the data in the database in order of fit to a questioned sample, and this it does extremely well. Once comparability ranking has been achieved, it is then necessary to visually compare the spectral fingerprint of the high comparability samples to the questioned sample to ensure that the fit is genuine and not an artifact based only on statistics. In addition to simply referring to the numbers (percentage comparability) it is also advisable to plot the percentage comparability relative to the specific sample giving that comparability and its positional number in the database. In this way significant breaks in slope and slope changes in the plot can be observed. These phenomena usually indicate the start of new populations and are a means of sorting data.

Principal component analysis

Principal component analysis (PCA) is a means of assessing the variability of the inter-relationships within a dataset. It is based on the concept of reducing dimensionality in multivariate data and plotting linear combinations of the response variables to explain patterns within the dataset. The defining characteristic of PCA is that its aim is to understand a dataset by considering a group of variables together rather than focusing on only one variable at the time. Fortunately, in datasets with many variables, groups of variables often move together. One reason for this is that more than one variable may be measuring the same driving principle governing the behavior of the system. PCA is a quantitatively rigorous method for achieving an indication of co-association of individual groups of samples. The method generates a new set of variables, called principal components. Each principal component is a linear combination of the original variables. All the principal components are orthogonal to each other so there is no redundant information. The principal components as a whole form an orthogonal basis for the space of the data.

The first principal component is a single axis in space. When each observation is projected on this axis, the resulting values form a new variable. And the variance is the maximum among all possible choices of the first axis. The second principal component is another axis in space, perpendicular to the first. Projecting the observations on this axis generates another new variable. The variance of this variable is the maximum among all possible choices of this second axis. By definition, the full set of the principal components is as large as the original set of variables. But it is commonplace for the sum of the variances of the first few principal components to exceed ~80% of the total variances of the original data. Examination of a few of these new variables can enable the development of a deeper understanding of the driving forces that generated the original data.

Linear discriminant analysis

Discriminant analysis is a method used to model the extent to which an observation belongs to a particular group. The data are described by a series of orthogonal vectors which are possible to graphically represent in a two-dimensional system using two of the determined vectors. The resulting data plot therefore graphically illustrates the presence of groups within the data. Discriminant analysis provides a statistically valid method to test the variation present within the data. This enables the discrimination of gold sources within a sample set. The discriminant analysis was undertaken using the SPSS for Mac statistical software using all analysed isotopes.

RESULTS AND DISCUSSION

In order to better understand the principle of gold spectral fingerprinting it is easier to detail the process by reference to a specific example. In this study, data are presented from an investigation into a possible gold theft where material was thought to have been removed from one or more of four mines in an area of ~400 km2. Gold was obtained from each of the mines in question to provide a reference database of samples and the recovered gold compared to results in this database. This investigation highlights the problems associated with gold fingerprinting as variations in the spectral fingerprint will be observed due to inclusions in depth in the gold. Although this aspect increases the complexity of data interpretation the specific fingerprint of the recovered gold is relatively easy to see and significant differences in elemental association patterns within the area can be identified to a level where provenancing is possible. The raw-count data for 44 elements for the stolen and reference gold samples are detailed in Figure 2. A comparability plot (Figure 3) is also detailed to give an indication of relative comparison of all samples in the database. The spectral plots (Figure 2a-e) represent sequentially the relative reproducibility of 39 samples of the recovered stolen gold, 12 samples from the suggested mine of origin (Reference Mine A), 11 samples from Reference Mine B, 12 samples from Reference Mine C and 12 samples from Reference Mine D.

As can be seen from these spectral plots there is an extremely good match between all samples from an individual mine batch. Furthermore, the visual match in the spectral fingerprint of samples shown in Figure 2a and b is excellent while matches between samples of stolen gold shown in Figure 2a with the other three reference mines is extremely poor.

A detailed comparability plot is shown in Figure 3 and the actual comparability percentages detailed in Table 1. Here, simply as an example, a single sample (Recovered gold S17) is matched with the database. The data in the resulting comparability plot (Figure 3) and data table (Table 1) indicate that there is a sliding match of between 99.64% and 97.14% for all recovered gold and all samples from Reference Mine A. At sample Reference Mine C4 (sample 53 in Table 1) there is a significant break in slope in the comparability graph (Figure 3) indicating the start of a completely different series of samples. As indicated previously, this break in slope represents the point where

Table 1 Comparability match for 'stolen' gold samples and reference mines.

Sample	Comparability %	Order	Sample	$Comparability \ \%$	Order	Sample	Comparability %	Order
Rec Gold S17	100	1	Mine A 10	98.45	30	Mine C 6	86.8	59
Rec Gold S17	100	2	Rec Gold S7	98.39,	31	Mine B 12	85.8	60
Rec Gold S29	99.6	3	Mine A 12	98.35	32	Mine C 9	85.5	61
Rec Gold S24	99.5	4	Mine A 11	98.29	33	Mine C 7	83.7	62
Rec Gold S1	99.3	5	Rec Gold S22	98.29	34	Mine B 3	82.7	63
Rec Gold S25	99.3	6	Rec Gold S11	98.26	35	Mine C 8	81.7	64
Rec Gold S14	99.3	7	Rec Gold S38	98.16	36	Mine C 10	81.2	65
Rec Gold S33	99.3	8	Rec Gold S12	98.11	37	Mine B 10	80.6	66
Mine A 4	99.2	9	Rec Gold S3	98.11	38	Mine B 9	79.7	67
Mine A 3	99.1	10	Rec Gold S16	98.07	39	Mine B 5	79.6	68
Rec Gold S20	99	11	Rec Gold S18	98.07	40	Mine B 8	79.2	69
Mine A 2	99	12	Rec Gold S32	98.05	41	Mine B 1	78.7	70
Rec Gold S35	98.9	13	Rec Gold S27	7 97.99	42	Mine B 2	76.5	71
Rec Gold S13	98.9	14	Rec Gold S6	97.98	43	Mine B 7	74.7	72
Rec Gold S5	98.9	15	Mine A 9	97.97	44	Mine B 4	72.6	73
Mine A 1	98.9	16	Rec Gold S28	97.84	45	Mine B 6	71.7	74
Rec Gold S21	98.8	17	Rec Gold S30	97.82	46	Mine B 11	71.4	75
Rec Gold S39	98.8	18	Rec Gold S34	97.8	47	Mine D 12	67.4	76
Mine A 5	98.8	19	Rec Gold S32	7 97.7	48	Mine D 4	63.2	77
Mine A 8	98.7	20	Rec Gold S1	5 97.7	49	Mine D 2	54	78
Rec Gold S2	98.7	21	Mine A 7	97.67	50	Mine D 1	47.4	79
Rec Gold S19	98.7	22	Rec Gold S2	3 97,52	51	Mine D 3	37.7	80
Rec Gold S26	98.7	23	Rec Gold S8	97.14	52	Mine D 10	34.4	81
Rec Gold S4	98.7	` 24	Mine C 4	89.51	53	Mine D 9	30.6	82
Rec Gold S31	98.7	25	Mine C 5	88.96	54	Mine D 5	22.6	83
Rec Gold S36	98.7	26	Mine C 3	88.11	55	Mine D 11	15.1	84
Rec Gold S9	98.6	27	Mine C 1	87.99	56	Mine D 8	13.9	85
Rec Gold S10	98.6	28	Mine C 11	87.68	57	Mine D 7	13.3	86
Mine A 6	98.6	29	Mine C 2	87.64	58	Mine D 6	0	87

Rec, recovered

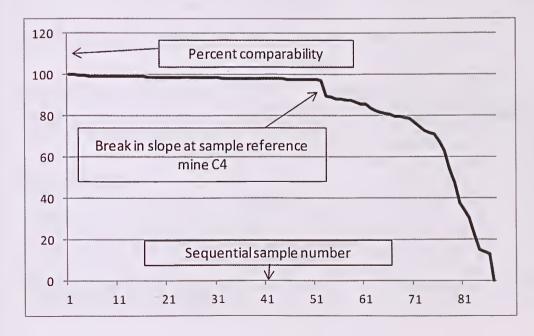
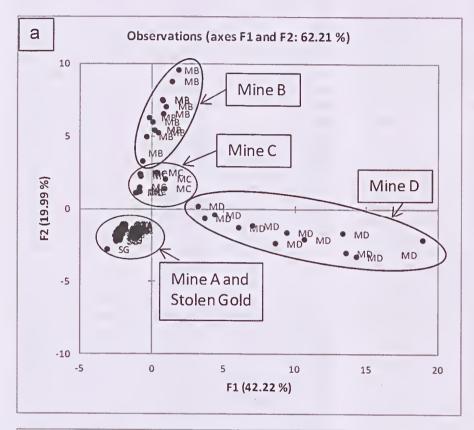


Figure 3 Comparability slope for case samples

it is possible to differentiate between gold from a different source to the reference gold. Consequently it can be inferred from this graph that all samples from Reference Mines B, C and D have a statistically insignificant chance of being co-provenanced with any samples in the so-called batch of stolen gold and represent completely different

mineralising events in the formational processes of the gold ore. When any other sample of gold from either Reference Mine A or stolen gold are compared in the same way an equivalent pattern is generated confirming the observation of co-provenance of samples from Reference Mine A and stolen gold.



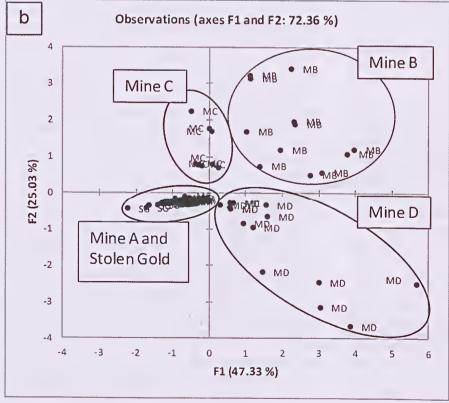


Figure 4 PCA plots for (a) all elements and (b) Pd, Mo, Co, Pb and Se.

Final confirmation of the association of Mine A samples with those of the stolen gold can be achieved by using PCA plots. In this case, it is possible to see by using both the total-element analytical cocktail (Figure 4a) and selected elements (Figure 4b) that the samples of stolen gold group extremely tightly with samples of gold from Mine A and are isolated form samples representing all three other mines. There is some apparent overlap between samples from Mines B and C (Figure 4a) and Mines C and D (Figure 4b). However, isolation of Mines C and D (Figure 4a) and Mines C and B (Figure 4b) allows isolation of these mines from each other and in all interpretational protocols detailed above, it is possible to isolate and unambiguously identify samples from all four mines.

CONCLUSIONS

Laser ablation-ICP-MS provides extremely sensitive analytical data for determining inter-element association patterns for gold samples. While it would be preferred that data were quantitative in nature, it is nonetheless easily possible to use relative raw counts, ternary association diagrams, linear discriminant analysis and principle component analysis to discriminate between the element association patterns of different deposits and thereby identify co-provenance or otherwise of samples. In addition the increase in the number of samples represented in in-house databases is becoming increasingly more important when identifying the generic provenance of samples that are not associated with a specific known mine of origin. When large databases are interrogated it is always possible to associate recovered material with a source, if that source is present on the database. Damage to gold is insignificant and the amount of material removed does not significantly reduce the value of the material. The fact that extremely small samples can be easily analysed also increase the ability to use extremely small samples, often present as microscopic material on floors, carpets and in clothing. Because such a small amount of material is used for analytical purposes, samples can always be provided to either defense or prosecution for corroborative analysis and can also be stored in a spatially very limited physical database for further research and method development.

ACKNOWLEDGEMENTS

We thank journal reviewers Richard Davy and Russell Frew for their helpful comments.

REFERENCES

- ABUZA Z 2003. Funding terrorism in South East Asia: the financial network of Al Qaeda and Jemaah Islamiya. Contemporary South East Asia 25, 169–199.
- BAERE M E & SCHNEIDER S 1990. Tracing illicit funds—money laundering in Canada. Solicitor General of Canada Report 1990-5.
- COETZEE B & HORN R 2011. The theft of precious metals from South African mines and refineries. *Institute of Securities Studies Monograph* 133.

- DE GOEDE M 2003. Hawala discourses and the war on terrorist finance. Environment and Planning (D): Society and Space 21, 513–532.
- EL QORCHI M, MAIMBO S M & WILSON J F 2003. Informal Funds Transfer Systems: an analysis of the informal hawala system. International Monetary Fund Washington DC.
- Freeman M J, Watling R J & Herbert H K 1994. Karpa Spring the Department of Minerals and Energy of Western Australia's role in a criminal fraud investigation. *Geological* Society of Australia Abstracts 37, 120–121.
- Gastrow P 2001. Theft from South African mines and refineries, the illicit market for gold and platinum. *Institute for Security Studies Monograph* 54.
- GROSSE R E 2001. Drugs and money: laundering Latin American cocaine dollars. Praeger Publishers, Westport.
- HERBERT H K & WATLING R J 1997. Chapter 88A Forensic gold analysis. *In:* Freckleton 1 & Selby H (eds) *Expert evidence*, pp. 8-4331–8-4457. Law Book Company, Sydney.
- JAMWAL N S 2008. Hawala—the invisible financing system of terrorism. Strategic Analysis 26, 181–198.
- Kogan V V, Hinds M W & Ramendik G I 1994. The direct determination of trace elements in gold and silver materials by laser ablation inductively coupled plasma mass spectrometry without matrix matched standards. Spectrochimica Acta 49B, 333–343.
- Levi M & Reuter P 2006. Money laundering. Crime and Justice 34, 289–375.
- LILLEY P 2003. Dirty dealing—the untold truth about global money laundering, international crime and terrroism. Kogan Page, London.
- Masciandaro D (Editor) 2004. Global financial crime: terrorism, money laundering and offshore centres. Global Finance Series, Ashgate Publishing, Aldershot.
- MILLARD G H 1999. Brazil: money laundering. Journal of Money Laundering Control 2, 365–371.
- Outridge P M, Doherty W & Gregoire D C 1998. Determination of trace element signatures in placer gold by laser ablation-inductively coupled plasma-mass spectometry as a potential aid for gold exploration. *Journal of Geochemical Exploration* 60, 229–240.
- REUTER P & TRUMAN E M 2004. Chasing dirty money: the fight against money laundering. Institute of International Economics, Washingtom.
- SHEHU A Y 1997. The Asian alternative remittance systems and money laundering. *Journal of Money Laundering Control* 7, 175–185.
- Sie S H, Murao S & Suter G F 1996. Trace element distribution in native gold. *Nuclear Instruments and Methods in Physics Research Section B* 109, 633–638.
- TAYLOR J J, WATLING R J, SHELL C A, IXER R A, CHAPMAN R J, WARNER R B & CAHILL M 1997. From gold ores to artefacts in the British Isles: a preliminary study of a new LA-ICP-MS analytical approach. *In:* Sinclair A J, Slater E A & Gowlett J (eds) *Archaeological Sciences 1995*, pp. 144–154. Oxbow Books, Oxford.
- WALKER J 1997. How big is global money laundering. Journal of Money Laundering Control 3, 25–37.
- WALKER J & UNGER B 2009. The Walker Gravity Model. Review of Law and Economics 5, 821–853.
- WARDE I 2007. The price of fear: AI-Qaeda and the truth behind the financial war on terror. I B Taurus and Co, London.
- WATLING R J 1996. Novel applications of laser ablation inductively coupled plasma mass spectrometry in inorganic analytical chemistry. Rapid Communications in Mass Spectrometry 10, 130–137.
- WATLING R J 1999. Novel applications of laser ablation inductively coupled plasma mass spectrometry (LA-ICP-MS) in the field of forensic science and forensic archaeology. Spectroscopy 14 (6), 16–34.

- Watling R J, Herbert H K, Barrow I S & Thomas A G 1995. Analysis of diamonds and indicator minerals for diamond exploration by laser ablation-inductively coupled plasma mass spectrometry. *Analyst* 120, 1357–1364.
- WATLING R J, HERBERT H K, DELEV D. & ABELL 1 D 1993. Gold fingerprinting by laser ablation inductively coupled plasma mass spectrometry. Spectrochimica Acta 49B, 305–319.
- WATLING R J, LYNCH B & HERRING D 1997. Use of laser ablationinductively coupled plasma-mass spectrometry (LA-ICP-MS) for fingerprinting scene of crime evidence. *Journal of Analytical Atomic Spectrometry* 12, 195–203.
- WILLIAMS P 1997. Money laundering. South African Journal of International Affairs 5, 71–96.
- WOOLNER A 1994. Washed in gold, the story behind the biggest money lanndering investigation in US history. American Lawyer Books, Simon and Schuster, New York.
- ZDANOWICZ J 2004. Detecting money laundering and terrroist financing via data mining. Communications of the Association for Computing Machinery 47, 53–55.
- ZELDIN M 1997. Money laundering. Journal of Money Laundering Control 1, 295–302.

Received 18 February 2013; accepted accepted 18 June 2013

Geochronology of the Archean of Western Australia: a historical perspective

R T PIDGEON 1* & M T D WINGATE 2

- ¹ Western Australian School of Mines, Curtin University, Kent Street, Bentley, WA 6102, Australia.
- ² Geological Survey of Western Australia, 100 Plain Street, East Perth, WA 6004, Australia.
- *Corresponding author 🖾 r.pidgeon@curtin.edu.au

The Yilgarn and Pilbara Cratons of Western Australia are amongst the largest segments of Archean crust on Earth. Unraveling the geological history hidden in these ancient rocks has been a major challenge, involving many years of geological fieldwork, geochemical and geophysical studies and, most significantly, the application of isotopic dating. In this contribution we present a brief overview of the role of isotopic dating in providing numerical measurements of the geological age of igneous and metamorphic events and resolving key questions on the evolution of the cratons. Our review begins with the building of the first mass spectrometer in the Physics Department at the University of Western Australia in the 1950s. We follow the rapid evolution of techniques and concepts of isotopic dating up to the present day when the integration of accumulated geochronological data provides a high-resolution record of Archean events in the Yilgarn and Pilbara Cratons. We highlight major achievements, including the identification of the oldest fragments of the Earth's crust in metasedimentary rocks of the Yilgarn Craton and the determination of the age of the world's oldest fossils in the Pilbara Craton. Isotopic dating and associated isotope geochemistry have increasing roles to play in resolving problems of crustal evolution and deep crustal structure in the Archean cratons of Western Australia.

KEYWORDS: Archean, geochronology history, isotopic dating, Pilbara Craton, Western Australia, Yilgarn Craton.

INTRODUCTION

The geology of Western Australia is dominated by two Archean cratons, the Pilbara in the north and the Yilgarn in the south (Figure 1), overlain by volcanosedimentary basins and surrounded and separated by Proterozoic orogenic belts. The two cratons are amongst the largest segments of Archean crust on Earth and are immensely important as a store of economic mineral deposits and for their unique preservation of early life and Hadean and Archean geological history. However, unraveling the geological history of the cratons is extremely challenging, especially in the Yilgarn Craton, where outcrop is scarce, deep weathering is common, and the correlation of noncontiguous greenstone and sedimentary units or igneous bodies is uncertain. This challenge has been largely met by the application of isotopic dating and isotope geochemistry. For example, Wyche et al. (2012) stated that ...of particular significance is the accumulating body of geochronological and isotope data that has allowed the major periods of crustal growth in the Yilgarn Craton to be identified'. A similar comment can be made for the Pilbara Craton. The story of isotopic dating is one of evolving technical advancement coupled with new concepts and applications, many of which were developed and tested on problems from the Archean of Western Australia. It is, therefore, most appropriate that a paper on the evolution of geochronological knowledge on the Archean of Western Australia is part of this centennial volume.

The present review follows in the footsteps of earlier historical reports on the contribution of isotopic dating to studies of the Archean rocks of Western Australia. Wilson et al. (1960) reviewed data from Peter Jeffery's laboratory at the University of Western Australia (UWA), and were the first to recognise the widespread occurrence of ~2700 Ma granitic rocks in the southwest of Western Australia. Compston & Arriens (1968) and Arriens (1971) summarised new K-Ar and Rb-Sr age determinations on Australian Precambrian rocks up until 1967, recognising at this early stage the contrast between the 3000-2900 Ma ages in the Pilbara Craton and the 2700-2600 Ma ages that predominate in the Yilgarn Craton. De Laeter & Trendall (1979) described the early history of geochronology from the discovery of radioactivity, the development of mass spectrometry from Aston to Nier, the early evolution of the U-Pb, K-Ar and Rb-Sr techniques, to the construction of the first mass spectrometer in Western Australia in the Physics Department at UWA. A further review in this journal by De Laeter (1994), on the occasion of receiving the Royal Society Medal for 1993, continued the theme of geochronology of the early Earth and described some highlights of research on the Archean of Western Australia since 1979, including the discovery of >4 Ga zircons in quartzites of the Narryer Terrane (Froude et al. 1983). Particularly valuable are his comments on early geochronological research at the Western Australian Institute of Technology (WAIT, later to become Curtin University) and the early history of Peter Jeffery's laboratory at UWA. Each of these reviews is exceptional in conveying the experiences of individuals involved in leading geochronological research at that time.

In this review, we briefly summarise material covered in earlier reviews and follow the history of geochronological research on the Archean of Western Australia up to the present day. A useful introduction to methods and concepts is provided by Kirkland & Wingate (2013). Photographs of some of the geochronologists who have made valuable contributions to the geochronology of the Archean of Western Australia are included in Figures 2 and 3. However, the proliferation of U-Pb zircon data in support of projects by the Geological Survey of Western Australia (GSWA) and Geoscience Australia (GA), the introduction of new dating and isotope technologies, and the wide range of contributions from Australian and overseas laboratories has made a comprehensive review impossible to achieve within the limitations of this article and we regret that some valuable contributions may not be accorded the recognition they deserve.

MILESTONES IN GEOCHRONOLOGY OF THE ARCHEAN OF WESTERN AUSTRALIA

Peter Jeffery's laboratory in the Department of Physics, UWA

In the early 1950s, little was known of the ages of geological events in the Yilgarn and Pilbara Cratons. Isotopic dating methods using thermal ionisation mass spectrometry (TIMS) were only just being developed in several laboratories in the USA [eg Rb-Sr (Aldrich et al. 1953); K-Ar (Wasserburg 1954); U-Pb (Tilton et al. 1955)]. Inspired by the potential of these new developments, Peter Jeffery, together with PhD student David Greenhalgh, assembled a Nier-type solid-source mass spectrometer, provided through a grant from the Department of Terrestrial Magnetism of the Carnegie Institution in Washington, in the basement of the Physics Building at UWA for the purpose of isotopic dating (Greenhalgh & Jeffery 1959). They were joined by William Compston, Glen Riley, and soon after, by John De Laeter, in pioneering research into the timing of geological events in the development of the Yilgarn and Pilbara Cratons.

Rb-Sr whole-rock dating

An important factor in the early success of the physics group from UWA was the collaboration with Alan Wilson from the UWA Geology Department. With Wilson to guide them in the field, the group undertook Rb-Sr dating of granites from the Darling Range Batholith in the hills to the east of Perth. Their discovery that the Rb-Sr age of a granite could be determined from a number of 'whole-rock' samples was a milestone in Rb-Sr geochronology (Compston & Jeffery 1959; Compston et al. 1960) and a major influence on geochronological studies of the Archean of Western Australia for 30 years. Their age of 2700 Ma for the granite at Canning Dam was the first precise age of a granite from the Yilgarn Craton. In 1960, Alan Wilson left UWA to take up the Chair of Geology at the University of Queensland and in 1964, Glen Riley took a position at the Australian Atomic Energy Commission at Lucas Heights. Bill Compston, who was by then on the UWA Physics staff, relocated to Canberra, to establish a Rb-Sr laboratory in the Department of Geophysics and Geochemistry at the Australian National University (ANU). These staff movements resulted in the

disbanding of the UWA geochronology group. Jeffery concentrated his further research on nuclear astrophysics and no geochronological measurements were made in Western Australia for almost a decade, although Compston continued Rb–Sr isotopic dating at ANU.

Isotopic dating at the Australian National University (ANU)

In 1961, Compston and his group at the ANU converted a Metropolitan-Vickers MS2 gas-source mass spectrometer to a solid-source instrument for Rb-Sr dating. In an early PhD study, Turek (1966) demonstrated that gold mineralisation at Coolgardie, Kalgoorlie and Norseman defined a Rb-Sr total-rock isochron of 2400 ± 40 Ma. Pieter Arriens, a PhD graduate from UWA, joined Compston and undertook a wideranging Rb-Sr whole-rock study of granites from the Yilgarn and Pilbara Cratons. A review of geochronological knowledge of the Yilgarn and Pilbara Cratons up to that time was presented at the 1967 International Conference of Precambrian stratified rocks in Edmonton (Compston & Arriens 1968). In addition to Rb-Sr dating, Virginia Oversby from ANU reported Pb-Pb isochron ages of 2760-2630 Ma, using K-feldsparplagioclase-total-rock samples, for eight intrusive bodies in the Kalgoorlie-Norseman area in the Yilgarn Craton (Oversby 1975).

In 1980 Malcolm McCulloch established a Sm-Nd laboratory at the ANU and applied the technique to dating Archean gneisses in the Yilgarn Craton (McCulloch et al. 1983 a, b). The success of Hamilton et al. (1979) in using the Sm-Nd whole-rock method to date Archean greenstones in South Africa raised the possibility that this technique could be used to date mafic rocks, a long-standing problem in geochronology. Dating the Archean greenstones of the Yilgarn Craton was the immediate challenge and McCulloch & Compston (1981) determined an isochron age of 2790 ± 30 Ma for the Kambalda greenstone sequence and also concluded, from the high initial 143Nd/144Nd, that the mantle had been highly depleted by the late Archean. However, Claoué-Long et al. (1984) questioned the McCulloch & Compston (1981) result for including associated sodic granites and a felsic porphyry in the isochron calculation and reported a re-determined Sm-Nd isochron age of 3262 ± 44 Ma for whole-rock samples of mafic-ultramafic lavas from the Kambalda area. This latter age was very controversial as it contradicted Pb isotope evidence suggesting the age of the lavas was close to 2700 Ma (Roddick 1984). This was finally resolved by a SHRIMP U-Pb age of 2692 ± 2 Ma on pyroclastic zircons from a chert unit within the greenstone sequence (Claoué-Long et al. 1988). The old whole-rock Sm-Nd date of Claoué-Long et al. (1984) was seen to be the product of mixing of unrelated rock components raising general questions on the application of the technique as a precise dating tool.

Dirk Nieuwland continued to operate the conventional U–Pb zircon laboratory and reported U–Pb zircon ages of ~3250 Ma for gneisses from the Toodyay district (Nieuwland & Compston 1981). In a rare application of K–Ar dating to Archean rocks of Western Australian, Wijbrans & McDougall (1987) reported ⁴⁰Ar–³⁹Ar ages of 2900–2840 Ma for metamorphic amphiboles from the eastern Pilbara Craton and interpreted them as

indicating prolonged high temperatures within the Shaw Batholith or else dating a later thermal pulse associated with the intrusion of post-tectonic granitoids.

Alec Trendall arrives at the Geological Survey of Western Australia (GSWA)

The appointment of Alec Trendall from the Geological Survey of Uganda to the position of petrologist at GSWA in 1962 was arguably the next milestone in the development of geochronology in Western Australia. Trendall had been mapping Archean rocks in Uganda and realised the necessity of having accurate geochronological data for understanding Archean geology. On the advice of Peter Jeffery, he began a long-term cooperation with Compston at the ANU on Rb–Sr dating of rocks from the Archean of Western Australia. With the start-up of isotopic dating at WAIT in 1968, Trendall initiated a program of Rb–Sr dating between geologists from the GSWA and the De Laeter group at

WAIT. During his long career at GSWA, where he served as Director from 1980 to 1986, Trendall remained a tireless advocate of geochronology.

Development of Thermal Ionization Mass Spectrometry (TIMS) at WAIT

The next important development in Archean geochronology was the appointment in 1968 of John De Laeter, a former student of Peter Jeffery, to head the newly established Physics Department at the Western Australian Institute of Technology (WAIT). One of his first actions was to purchase a 12 inch radius, MS12 solid-source mass spectrometer and build a Rb–Sr dating laboratory. Later that year he formed a close working relationship with Alec Trendall, where GSWA field geologists submitted samples of Archean rocks from the Yilgarn and Pilbara for Rb–Sr dating (Muhling & De Laeter 1971; De Laeter *et al.* 1975, 1981b; De Laeter & Baxter 1987).

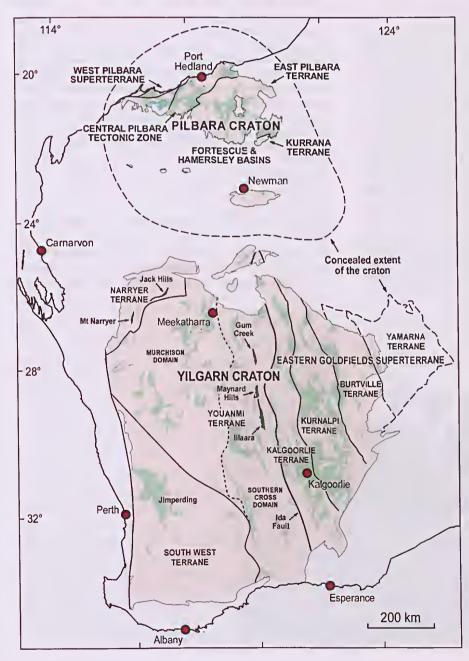


Figure 1 The Archean Yilgarn and Pilbara Cratons of Western Australia, and their terrane subdivisions (Yilgarn: Cassidy et al. 2006; Pawley et al. 2012; Pilbara: Hickman & Van Kranendonk 2012a, b), Localities shown include the Jack and Mt Narryer, the Jimperding metamorphic belt, and the Gum Creek, Illaara, and Maynard Hills greenstone belts. Revised extent of the Pilbara Craton is from Hickman & Smithies, in prep.

Pb-Pb geochronology at the University of Western Australia (UWA)

In another landmark development in 1978, Hazel Chapman, with Michael Bickle and Neal McNaughton, set up a Pb-Pb laboratory at the Department of Geology at UWA. Samples were prepared at UWA and mass spectrometry was undertaken at WAIT. Pb-Pb studies included the report of a ~2700 Ma age for gneisses from the Diemals area north of Southern Cross (McNaughton & Bickle 1987). The group also studied the Pb-Pb geochronology of granite plutons in the Pilbara Craton (Bickle et al. 1989). Bickle and Chapman returned to the UK late in 1982, leaving McNaughton to carry on the laboratory within the Key Centre for Strategic Mineral Deposits headed by David Groves. Research focused on investigating the ages and origin of Yilgarn mineralisation (McNaughton & Cassidy 1990; McNaughton & Groves 1996) and included results of student theses (Perring & McNaughton 1990, 1992).

Sm-Nd and zircon U-Pb dating at WAIT

In 1978, lan Fletcher joined the WAIT group as a research fellow on an ARC grant to Kevin Rosman and Alec Trendall to establish a Sm–Nd dating laboratory. Projects included a number of Sm–Nd model-age traverses across the Yilgarn Craton (Fletcher & Rosman 1984; Fletcher *et al.* 1983, 1985). In a landmark paper, De Laeter *et al.* (1981a) reported a 3348 ± 43 Ma Rb–Sr whole-rock age, supported by Sm–Nd age results, for banded gneisses near Mt Narryer in the northwest Yilgarn Craton, identifying the Narryer region as a uniquely old part of the Yilgarn Craton. De Laeter *et al.* (1985) reported Sm–Nd T_{CHUR} model ages of ~3.7 Ga for the Meeberrie Gneiss in the Mt Narryer area and ~3.54 Ga for a sheet of Dugel Gneiss within the Meeberrie Gneiss.

In 1982, Robert Pidgeon joined the WAIT group and set up a conventional TIMS U-Pb laboratory for zircon geochronology. Research in collaboration with Simon Wilde, who had recently joined WAIT from the GSWA,

focused on greenstone belts in the western Yilgarn Craton, including the Saddleback and Wongan Hills belts, and identified two ages of greenstone volcanism—at ~3000 and ~2700 Ma—in the Youanmi and South West Terranes of the Yilgarn Craton (Wilde & Pidgeon 1986; Pidgeon *et al.* 1990).

Advent of SHRIMP at the ANU

The inability of first-generation ion microprobes to resolve Pb isotopes from unwanted molecular interferences in lunar samples led Compston, together with his former student S W Clement, to initiate a project in the early 1970s to build a high-resolution ion microprobe at the ANU Research School of Earth Sciences (Clement et al. 1977). The instrument, known as the Sensitive High Resolution Ion Microprobe (SHRIMP), had a working mass resolution of over 5000 and could easily resolve the isotopes of Pb from most isobaric interferences. This instrument was revolutionary in that static analyses could be made on 10-20 µm diameter spots on selected parts of zircon crystals, allowing inherited and disturbed parts to be avoided and leading to uncomplicated age determinations. Also, the speed of analysis meant that a large number of zircons could be analysed in a short time. With this new capability, it became possible to determine the distribution of detrital zircon ages in sedimentary samples, a task impractical using slow conventional TIMS techniques. Ireland et al. (2008) provided a comprehensive history of the development of SHRIMP 1, from 1975 to 1980, and its commissioning in 1983. This instrument was to fundamentally change U-Pb zircon geochronology worldwide.

Hadean zircons discovered at Mt Narryer and the Jack Hills

The first project undertaken using the SHRIMP I ion microprobe was an investigation of the ages of detrital zircons in a conglomerate from Mt Narryer (Figure 1), an



Figure 2 Geochronologists in 1987 on the outcrop of Jack Hills metaconglomerate sample W74, which contains zircons with ages in excess of 4.0 Ga. From left to right: M T McCulloch, D R Nelson, W Compston, R T Pidgeon, I R Fletcher, S A Wilde and I S Williams.

area in the northwestern corner of the Yilgarn Craton already known to be extremely old from the Rb–Sr results of De Laeter *et al* (1981a, 1985). Samples were provided by Ian Williams and John Myers of the GSWA. The amazing discovery of a small number of zircon grains with ages greater than 4 Ga (Froude *et al.* 1983) focused worldwide attention on this area of the Yilgarn Craton and demonstrated the unique analytical capacity of the SHRIMP.

In the 1980s, Robert Pidgeon from WAIT and later Neal McNaughton from UWA took Archean zircon samples to Canberra for analysis on the SHRIMP. An important result of this research was the discovery of detrital zircons with ages >4.2 Ga in a quartz-pebble conglomerate from the Jack Hills (Figures 1, 2) (Compston & Pidgeon 1986) confirming the earlier results from Mt Narryer and extending the distribution of very old zircons. At the time, the reality of the old ages was questioned in the literature and doubts were raised about the integrity of the new SHRIMP (Schärer & Allegre 1985). However, these doubts were put to rest by reports of >4 Ga ages for Jack Hills zircons determined by singlezircon Pb-evaporation by Kober et al. (1989) of the University of Heidelberg in Germany, and by TIMS U-Pb analysis by Amelin (1998), then at the Royal Ontario Museum. The discovery of ancient zircons at Jack Hills foreshadowed extensive studies of the old grains by isotope and geochemical techniques, because these grains were the only known surviving fragments of the Hadean period of Earth's history (De Laeter & Trendall 2002; Wilde & Spaggiari 2007).

Geochronological research then focused on the old gneisses surrounding the conglomerates in an attempt to locate the parent rocks of the >4 Ga zircons. Kinny et al. (1988) from the ANU reported SHRIMP U-Pb zircon ages of 3678 ± 6 Ma for the monzogranitic Meeberrie Gneiss (Myers & Williams 1985), 3381 ± 22 Ma for the leucosyenogranitic Dugel Gneiss, and 3730 ± 6 Ma for meta-anorthosite of the Manfred Complex. Fletcher et al. (1988) reported a Sm-Nd, Pb-Pb, and Rb-Sr age of ~3.69 Ga for the Manfred Complex. Nutman et al. (1991) from the ANU reported the results of a comprehensive SHRIMP U-Pb study of zircons from the Narryer Gneiss Complex including an age of 3731 ± 4 Ma for a tonalite of the Meeberrie Gneiss. Kinny & Nutman (1996) emphasised that it is impossible to quote a single age for the Meeberrie Gneiss in the Mt Narryer region as it is a polyphase migmatite that has been metamorphosed to granulite facies, with ages ranging from 3730 to 3300 Ma. Nutman et al. (1993) used U-Pb zircon geochronology and Nd isotope geochemistry to map gneiss units of different ages in the Narryer Gneiss Complex, recognising a ~100 km wide tract of 3700-3300 Ma gneisses, flanked by 3000-2900 Ma gneisses, and all intruded by 2750-2620 Ma granites. Granites from near the Jack Hills showed complex zircon U-Pb systems but recorded age peaks at 3.75-3.65, 3.50 and 3.3 Ga (Pidgeon & Wilde 1998).

Research has continued on the old zircons from Mt Narryer and the Jack Hills using a variety of isotopic and chemical techniques, and the list of publications is too great to be covered in detail in this short overview. Maas & McCulloch (1991) investigated the U-Pb age, Nd isotopes, and REE chemistry of Jack Hills zircons and

concluded they originated within a felsic parent rock. A notable contribution was that of Crowley *et al.* (2005) who made an ICPMS U–Pb age study of zircons from several outcrops of metaconglomerate and quartzite in the Jack Hills and Mt Narryer area and identified different trends in the age spectra which bear on the provenance of the zircons. Research groups from the University of Wisconsin, in association with Simon Wilde from Curtin University, and University of California, Los Angeles, in association with Robert Pidgeon of Curtin University, identified isotopically-heavy oxygen in the >4 Ga zircons and interpreted this as evidence for the existence of oceans on Earth ~4.3 Ga years ago (Wilde *et al.* 2001; Peck *et al.* 2001; Mojzsis *et al.* 2001; Valley *et al.* 2002; Cavosie *et al.* 2005).

SHRIMP II installed at Curtin University

A major landmark in the ongoing geochronological investigation of the Yilgarn and Pilbara Cratons was the initiative by John De Laeter to form a consortium comprising Curtin, GSWA and UWA, for the purpose of purchasing the first commercial SHRIMP instrument, SHRIMP II. University and GSWA funding was supplemented by a large equipment grant from the Australian Research Council. The SHRIMP II was installed at Curtin University in 1993 and Allen Kennedy was appointed as manager of the SHRIMP facility (De Laeter & Kennedy 1998). A second SHRIMP was installed at Curtin in 2003 under the umbrella of the Federal Government's Systemic Infrastructure Initiative, with support from the Government of Western Australia. With these instruments, zircon U-Pb geochronological research into the Archean of Western Australia accelerated rapidly.

SHRIMP U-Pb dating at GSWA

Another landmark decision that greatly enhanced geochronological research in the Yilgarn and Pilbara Cratons was the 1989 appointment of a geochronologist, Ian Fletcher, at GSWA to support its field program. He utilised primarily the Sm–Nd technique. However, as partners in the new SHRIMP, U–Pb zircon geochronology became a prominent tool at GSWA, and David Nelson, a recent graduate from the ANU, was appointed as the GSWA geochronologist in 1990, following Ian's departure.

GSWA has published an annual compilation of SHRIMP geochronological results since 1995. The first report, Nelson (1995), described results obtained in 1994, and included 26 SHRIMP U-Pb zircon analyses on felsic intrusive and extrusive rocks of the Eastern Goldfields. Nelson (1997a) reported SHRIMP measurements on 35 zircon samples, which revealed that felsic volcanic rocks were erupted in the southern part of the Eastern Goldfields between 2713 and 2672 Ma and were intruded by coeval granite sheets. Between 1995 and 2005, GSWA published more than 400 Geochronology Records that describe results for Archean samples dated by David Nelson.

An exceptional discovery made in this period was the presence of >4.0 Ga zircon xenocrysts in two late Archean granites from the Narryer Terrane and the Murchison Province (Nelson 1996, 1997c). The core of xenocrystic grain 11 from the ~2636 Ma granitic gneiss at Churla Well in the Narryer Terrane produced a ²⁰⁷Pb/²⁰⁶Pb age of

 4183 ± 6 Ma (Nelson *et al.* 2000). The significance of this discovery in terms of the source rocks of the ancient zircons and of early crustal processes has not been resolved.

Also in this period, SHRIMP measurements of detrital zircons from quartzitic metasedimentary rocks in the Gum Creek, Maynard Hills and Illaara greenstone belts of the Southern Cross Domain (Figure 1) identified new sources of >4 Ga zircons (Wyche *et al.* 2004; Nelson 2005; Thern & Nelson 2012). Although it was previously thought that the ancient zircons were confined to the Narryer Terrane, these new discoveries extended the range of >4 Ga zircons to metasedimentary rocks in the centre of the Yilgarn Craton.

Nelson left GSWA in 2004 and was replaced by Curtin PhD graduate Simon Bodorkos. He was joined in August 2005 by Michael Wingate, a PhD graduate from the SHRIMP group at the ANU, then employed at the Tectonics Special Research Centre at UWA. Bodorkos left GSWA in 2007 to continue geochronology at Geoscience Australia, and Chris Kirkland joined GSWA as a geochronologist in 2008. Kirkland also brought experience in using isotopes such as Lu-Hf and Sm-Nd to explore crustal evolution. Wingate and Kirkland have expanded GSWA's extremely successful geochronology program; the Survey has so far published about 1150 Geochronology Records (mainly SHRIMP U-Pb zircon ages of individual rock samples), of which slightly more than half represent Archean rocks of the Yilgarn and Pilbara Cratons.

Ongoing isotopic dating of the Yilgarn Craton

In further studies, Nemchin & Pidgeon (1997) reported SHRIMP U-Pb zircon results for the Darling Range granites, concluding that they were emplaced between 2648 and 2626 Ma, and showing that the zircons contained 2690–2650 Ma cores. Schiøtte & Campbell (1996), at the ANU, reported zircon ages of 2716–2696 Ma for granites within greenstone belts in the Mt Magnet area and 2710

and 2694–2640 Ma for external granites. Wiedenbeck & Watkins (1993) reported similar ages of 2641 ± 5 and 2602 ± 14 Ma for post-folding granites from the same region. The ages of volcanism in the Murchison Domain, at 2.76–2.72 Ga (Pidgeon & Hallberg 2000), are comparable with zircon ages of ~2.73 Ga for felsic volcanic rocks from the Marda Complex (Pidgeon & Wilde 1990), but are marginally older than the ~2.71–2.67 Ga volcanic activity in the Eastern Goldfields (Nelson 1997b). The 1998 PhD thesis of Qi Wang at ANU provided an extensive dataset of new geochronological results for Archean granites and volcanic rocks, mainly from the Murchison and Southern Cross Domains (Wang 1998).

Between 2000 and 2008, several universitygovernment projects generated an impressive amount of geochronology data for the Yilgarn Craton. Fifty-two ages were published for Archean rocks as part of the Norseman-Wiluna Synthesis Project, a collaboration between Geoscience Australia (GA) and UWA aimed at providing geochronological constraints on geodynamic and tectonic models for the Eastern Goldfields (Fletcher et al. 2001; Dunphy et al. 2003). Another comprehensive research project, funded by the Minerals and Energy Research Institute of Western Australia (MERIWA), on the characterisation and metallogenic significance of Archean granitoids, included U-Pb zircon and titanite ages, and Sm-Nd and Pb-Pb results, for 60 granites across the Yilgarn Craton (Fletcher & McNaughton 2002). GA published U-Pb zircon results for 14 granites in the Eastern Goldfields and 13 in the South West Terrane (Sircombe et al. 2007). Kositcin et al. (2008) reported the results of a project funded by the Australian Minerals Industry Research Association (AMIRA), including 35 U-Pb zircon ages for metavolcanic and metasedimentary rocks in the Eastern Goldfields.

Zircon provenance studies

The ability of the SHRIMP ion microprobe to conduct a large number of U-Pb zircon analyses in a short time



Figure 3 Geochronologists in 2013 in the SHRIMP laboratory at Curtin University. From left to right: P D Kinny, M T D Wingate, A I S Kemp, N J McNaughton and C L Kirkland.

(~15 minutes per analysis) has opened the way for provenance studies based on surveys of the age distribution of detrital zircons. This is best illustrated by the studies of the zircons in quartzites from Mt Narryer (Froude et al. 1983; Crowley et al. 2005; Pidgeon & Nemchin 2006) and the Jack Hills (Dunn et al. 2005) (Figure 1). These studies demonstrated that detrital zircons in these samples consist of two main age components: a main group with ages between 3.7 and 3.0 Ga and a subordinate group with ages between 4.37 and 3.9 Ga. SHRIMP provenance studies of detrital zircon suites from quartzites from elsewhere in the Yilgarn Craton (Kinny 1990; Bosch et al. 1996; Pidgeon et al. 2010) found that the quartzites of the Jimperding Metasedimentary Belt (Figure 1), which resemble quartzites of the Narryer Terrane, contain detrital zircons with ages between 3.8 and 3.0 Ga, but none older than 4 Ga, suggesting that the source rocks of the ancient zircons were not present in the provenance of the Jimperding sediments.

Early geochronology of the Pilbara Craton

Early research in the Pilbara Craton (Figure 1) was constrained by its remoteness and the lack of detailed geological maps, until publication of the GSWA mapping, starting with Hickman & Lipple (1975). The earliest determination of an Archean age for the Pilbara Craton was a $^{207}Pb/^{206}Pb$ age of 2790 \pm 25 Ma for tanteuxenite from Woodstock, determined in the mass spectrometry laboratory at UWA (Greenhalgh & Jeffery 1959). An early outcome of close relationships developed between the Bureau of Mineral Resources (now GA), GSWA, and the ANU was the report by Leggo et al (1965) of Rb-Sr whole-rock ages of ~3000 Ma for a granite and felsic volcanic rocks from the Pilbara Craton. As a result of the cooperation between the WAIT group and GSWA, De Laeter & Trendall (1970) reported a Rb-Sr whole-rock isochron date of 2880 ± 66 Ma for the Copper Hills Porphyry. De Laeter and Blockley (1972) reported a Rb-Sr whole-rock isochron age of 3125 ± 366 Ma for foliated granitic gneiss near Marble Bar and 2670 ± 95 Ma for the Moolyella Monzogranite. They concluded from the initial 87Sr/86Sr that the granitic gneiss was close to primary crustal material whereas the Moolyella Monzogranite consists of reworked material. De Laeter et al. (1975) reported a well defined Rb-Sr whole-rock isochron age of 2951 ± 83 Ma for gneissic granite from the Shaw Granitic Complex and 2606 ± 128 Ma for the Cooglegong Monzogranite which intrudes the batholith.

In 1974, Virginia Oversby at the ANU undertook a program of research on common-Pb mineral systems and reported Pb–Pb data for whole-rock and feldspar samples from gneissic granites along the Mt Newman railway line, which showed that primary ages of granite domes were in the order of 2950 Ma, whereas a number of the samples showed signs of secondary disturbance (Oversby 1976).

Old age of the Big Stubby lead

The first evidence of an exceptionally old age for the Warrawoona Group of the Pilbara Craton was the report by Sangster & Brook (1977) of the isotopic composition of Pb from the Big Stubby deposit in the Duffer Formation near Marble Bar. They found that this Pb has the most

primitive isotopic composition of any conformable Pb and estimated its age at ~3500 Ma from the Stacey-Kramers Pb-evolution model (Stacey & Kramers 1975). In 1977, Pidgeon established an isotope dilution TIMS U-Pb laboratory at the Research School of Earth Sciences at the ANU and published a zircon age of 3452 ± 16 Ma for dacite of the Duffer Formation within the Warrawoona Group (Pidgeon 1978a), recently mapped by Hickman & Lipple (1975). This result confirmed the antiquity of the Warrawoona Group indicated by the Pb composition of the Big Stubby deposit (Sangster & Brook 1977) and was the first precise age determined on the volcanic succession of the Warrawoona Group. Further Pb isotope studies of galena by Richards et al. (1981) corroborated the primitive isotopic compositions of the Pilbara conformable leads.

Dating of granites and greenstones in the Pilbara

Geochronological research continued on the Pilbara granites. The first age determination on the Mt Edgar Granitic Complex was the 2670 ± 95 Ma Rb–Sr isochron age for the Moolyella Monzogranite (De Laeter & Blockley 1972). Compston & Arriens (1968) used 12 samples of the Mt Edgar Granitic Complex to obtain a Rb-Sr age of ~3050 Ma; this was later recalculated by De Laeter to 3279 ± 169 Ma (Hickman 1983). Pidgeon (1978b) reported a U-Pb zircon age of 3280 ± 20 Ma for a granodiorite sample from this batholith. Williams & Collins (1990) reported SHRIMP U-Pb zircon ages of ~3440 Ma for the oldest gneissic part of the Mt Edgar Granitic Complex and ~3310 Ma for younger posttectonic phases of the batholith. The similarity of these ages with those of volcanism led these authors to propose that granite-greenstone terranes in the Pilbara Craton represented coeval volcano-plutonic complexes.

McNaughton *et al.* (1988) obtained a date of 3578 ± 2 Ma for gabbroic anorthosite in the Shaw Granitic Complex. Bickle *et al.* (1989) reported Pb–Pb ages of ~2966 Ma for younger granite plutons in the same batholith and Bickle *et al.* (1993) reported Pb–Pb results confirming the ~3450 Ma age of a major component of the batholith and identifying a minor component at 3338 ± 52 Ma. The North Pole Monzogranite, which intrudes greenstones 20 km north of the Shaw Granitic Complex, was dated at 3459 + 18 Ma (TIMS U–Pb zircon age) by Thorpe *et al.* (1992).

Models for the evolution of the region were reviewed by Hickman (1981). Critical to these models were geochronological constraints on relationships between the granites and the volcanic successions. Pidgeon (1984) reported U-Pb zircon ages for the Boobina and Spinaway Porphyries of 3307 \pm 19 and 2768 \pm 16 Ma, respectively. The Boobina Porphyry intrudes greenstones of the upper Warrawoona Group, and the Spinaway Porphyry intrudes lower units of the unconformably overlying volcanic and sedimentary rocks of the Fortescue Group. Barley & De Laeter (1984) reported a Rb-Sr whole-rock age of 3471 ± 125 Ma for volcanic rocks equivalent to the Duffer Formation, and De Laeter & Martyn (1986) reported a Rb-Sr whole-rock age of 3234 ± 117 Ma for molybdenum-copper mineralisation at Coppins Gap. McCulloch et al. (1983) obtained Sm-Nd model ages of 3430 and 3400 Ma for felsic volcanic rocks of the Duffer Formation.

Thorpe et al. (1992) published the results of a comprehensive isotope dilution TIMS U-Pb zircon investigation, conducted at the Geological Survey of Canada, of Archean felsic units in the Marble Bar region. They found that felsic volcanic rocks of the Warrawoona Group, from the Duffer Formation upwards but with the exception of the Wyman Formation, were deposited in a restricted time period between 3471 and 3449 Ma. U-Pb zircon results from the Wyman Formation defined an age of 3325 ± 3 Ma, indicating a younger volcanic episode. Horwitz & Pidgeon (1993) reported a zircon age of 3.1 Ga for a tuff from the Sholl Belt in the west Pilbara, demonstrating that these volcanic rocks were distinctly younger than volcanic rocks of the Marble Bar region. The SHRIMP U-Pb zircon age of 3515 ± 3 Ma for volcanic rocks of the Coucal Formation of the Warrawoona Group (Buick et al. 1995) is the oldest age reported so far for volcanism in the Pilbara Craton.

In a major contribution, Alec Trendall applied SHRIMP zircon geochronology to establish the age of the banded iron-formations of the Hamersley Group of the Mt Bruce Supergroup, which overlies granite–greenstone basement of the Pilbara Craton (Trendall *et al.* 1998). This work demonstrated continuous deposition in the Fortescue and Hamersley Basins for at least 325 million years, from 2775 to 2450 Ma (Trendall & Blockley 2004).

Dating the world's oldest fossils and oldest terrestrial impacts

Stromatolites in cherts of the Dresser Formation of the Warrawoona Group are the world's oldest known fossils (Walter *et al.* 1980; Van Kranendonk *et al.* 2008). The Dresser Formation underlies the Duffer Formation, for which TIMS U–Pb analyses of zircon from two localities indicated upper intercept dates of 3471 ± 5 Ma and 3465 ± 3 Ma (Thorpe *et al.* 1992). These results represent a minimum age for the fossils. SHRIMP analysis of detrital zircons from a felsic volcaniclastic sandstone in the lower chert–barite unit of the Dresser Formation defined a dominant 3525 Ma age component. However one concordant grain has a ²⁰⁷Pb/²⁰⁶Pb date of 3481 ± 3 Ma, which is interpreted as a maximum age for deposition of the Dresser Formation and for the stromatolites (Wingate *et al.* 2009).

The Antarctic Creek Member of the Mt Ada Basalt, which lies beneath the Duffer Formation but above the Dresser formation, is notable for containing spherulebearing layers that represent the world's oldest recognised terrestrial impacts (Lowe & Byerly 1986; Glikson et al. 2004). Byerly et al. (2002) reported a SHRIMP date of 3470 ± 2 Ma for euhedral zircons from the Antarctic Creek Member spherule-bearing unit, which agrees within uncertainty with the age of the Duffer Formation. They interpreted the zircons as detrital grains derived locally from coeval or slightly older felsic igneous rocks rather than as material from the impact target and considered the date to approximate the depositional age of the cherts. Most remarkably, Byerly et al. (2002) obtained an identical result for a comparable spherule-bearing layer in the Barberton greenstone belt in South Africa.

Hf isotopes in Jack Hills zircons

The application of the 176Lu-176Hf decay system to ancient

detrital zircons from the Jack Hills as a means of investigating the earliest processes on Earth is another recent development in the application of geochronological techniques to the Western Australian Archean. Hafnium, as Hf⁴⁺, and zirconium, as Zr⁴⁺, have very similar ionic radii (0.84 and 0.83 Å, respectively), hence hafnium is a significant component in zircon (typically up to 2% in granitic zircons). Lu is also present in zircon, but only at the ppm level, so the radiogenic ¹⁷⁶Hf in zircon closely represents the Hf isotopic composition of the source magma. Studying this system in the ancient Jack Hills zircons provides information on the nature of the Hadean parent magmas.

The first investigation of Hf isotopes in the ancient zircons, by Amelin et al. (1999), reported the analyses of 37 zircons from Jack Hills conglomerate sample W74. They concluded that no zircons showed any evidence of an early depleted mantle and that the crust was a significant age when the zircons grew. In contrast, Harrison et al. (2005) and Blichert-Toft & Albaréde (2008) reported Hf results that indicated a widespread depleted mantle. However, Kemp et al. (2010), from a combined Hf and Pb study of 68 Jack Hills zircons, found no evidence in support of a strongly depleted Hadean mantle, in agreement with Amelin et al. (1999). They interpreted their data to suggest that Hadean source reservoirs generated granitic magmas throughout the Archean, supporting the notion of a long-lived and globally extensive Hadean protocrust that may have comprised the nuclei of some Archean cratons (Kemp et al. 2010).

Geochronological framework of the Pilbara and Yilgarn Cratons

Owing to the constraints of this review, only a brief summary can be made here of the geochronological knowledge of the Archean cratons of Western Australia. Readers interested in the detailed geochronology are referred to recent overviews of the geological history of the Yilgarn Craton (Kositcin *et al.* 2008; Wyche *et al.* 2012; Van Kranendonk *et al.* 2010, 2013) and the Pilbara Craton (Hickman & Van Kranendonk 2012a, b).

The exposed Pilbara Craton (Figure 1) has been divided into five granite-greenstone terranes (East Pilbara Terrane, West Pilbara Superterrane, comprising the Regal, Karratha and Sholl Terranes, and the Kurrana Terrane) and five principal volcanosedimentary basins (Hickman & Van Kranendonk 2012a, b). The extensive U-Pb zircon dataset now available for Pilbara rocks has resulted in closely controlled geochronological correlation of volcanic and granitic activity within the craton. Granite-greenstones in the Pilbara terranes have been dated at 3.52 to 3.07 Ga, formation of basins from 3.02 to 2.93 Ga, and post-orogenic granites from 2.89 to 2.83 Ga. The overlying Fortescue, Hamersley and Turee Creek Groups represent a 2.78-2.42 Ga succession of interbedded clastic and chemical sedimentary and volcanic rocks (Hickman & Van Kranendonk 2012a, b).

The Yilgarn Craton (Figure 1) is divided into the South West, Youanmi and Narryer Terranes and the Eastern Goldfields Superterrane (Cassidy *et al.* 2006). The Narryer Terrane contains the oldest rocks in the craton (>3.7 Ga), and the ~3.0 Ga quartzitic metasedimentary rocks at Mt Narryer and the Jack Hills contain detrital zircons with

ages from 4.37 to 3.90 Ga. The Youanmi Terrane is divided into the Murchison and Southern Cross Domains, and includes ~3.0 and 2.8–2.7 Ga greenstone belts within vast areas of 2.8–2.6 Ga granitoids. In the Southern Cross Domain, quartzitic metasedimentary rocks in the Gum Creek, Maynard Hills and Illaara Greenstone Belts (Fig. 1) contain zircons with ages from 4.35 to 3.90 Ga (Wyche *et al.* 2004). The South West Terrane also has ~3.0 and 2.7 Ga greenstone belts isolated within vast areas of 2.7–2.6 Ga granites. However, the ~3.0 Ga quartzitic metasedimentary rocks do not contain detrital zircons older than 3.6 Ga (Pidgeon *et al.* 2010).

In the Eastern Goldfields Superterrane (Fig. 1), which includes the Kalgoorlie, Kurnalpi, Burtville, and Yamarna Terranes, four main periods of volcanism and granite emplacement have been recognised at 2970-2910, 2815-2800, 2775-2735 and 2715-2620 Ma (Pawley et al. 2012; Wyche et al. 2012). Mole et al. (2012) reported patterns of granite formation ages in the southern Yilgarn Craton, highlighting distinct periods of granite formation followed by quiescence from ~3.0 to 2.6 Ga. The ages broadly decrease from west to east and appear to follow a pattern of progressively increasing activity culminating in a final, voluminous granite magmatic event at 2650 to 2620 Ma (Mole et al. 2012). The eastern Yilgarn Craton exhibits younger Nd model ages compared to those in terranes west of the Ida Fault, indicating that the crust forming the Eastern Goldfields Superterrane is younger and significantly more juvenile than the western Yilgarn Craton, which comprises older, reworked crust (Champion & Cassidy 2007; Wyche et al. 2012; Mole et al. 2013). This has profound implications for mineral exploration and is an exceptional outcome underpinning the value of building regional datasets of Nd and other isotopes, such as Lu-Hf (Kirkland et al. 2011).

Future isotopic dating studies of Archean cratons of Western Australia

The immediate future of geochronological studies of the Archean rocks of Western Australia will see an expansion of the regional zircon U–Pb dataset, to refine the geochronological framework of the cratons and focus on specific problems of ore genesis or tectonic boundaries. There will also be further studies of the old rocks and old zircons to elucidate the Hadean history of the Yilgarn Craton and of the Earth itself. Recent SHRIMP dating by Tony Kemp at UWA obtained a unimodal 3752 Ma zircon age for a well-preserved meta-anorthosite of the Manfred Complex near Mt Narryer (Tony Kemp pers. comm. 2013), now the oldest known rock in Australia.

More emphasis will be directed towards dating the mafic components of greenstone belts, following the recognition that many mafic intrusive rocks can be dated successfully using zircons found in felsic differentiates, or using baddeleyite (ZrO₂) in coarse-grained, weakly or non-metamorphosed gabbro or dolerite (Wingate 1999). This approach has identified suites of large, ~2.8 Ga mafic-ultramafic intrusions that make up to 40% by volume of greenstones in the northern Murchison Domain and host important V and PGE mineralisation (Ivanic et al. 2010). Similar ages for gabbros in the Southern Cross Domain (Wingate et al. 2011) and Burtville Terrane (Pawley et al. 2012), suggest the possibility of a 2.8 Ga Yilgarn-wide event, but no

significant mafic rocks of this age have so far been found in the intervening Kalgoorlie or Kurnalpi Terranes.

New studies by Ian Campbell, Yuri Amelin, and students at ANU are following up SHRIMP or laserablation ICPMS U-Pb analyses with chemical abrasion and ultra-high-precision TIMS analyses of the same zircons, to address the need for the extreme time resolution (sub-million-year precision: Amelin & Davis 2006) necessary to understand greenstone belt evolution and solve stratigraphic issues in the Eastern Goldfields, where many events—including mineralisation—occurred in only a few million years. TIMS U-Pb geochronology is currently undergoing a resurgence in Perth, thanks to renewed interest by Steve Denyzsyn (UWA), Alexander Nemchin (Curtin) and GSWA.

With the increasing spatial coverage of the zircon U-Pb database, further studies of patterns and regional trends of ages, inherited components, Th/U ratios, and radiation damage will provide key information on the thermal history and deep structure of the cratons. The database also includes Sm-Nd, Lu-Hf, Pb, Ar-Ar and Rb-Sr datasets, as well as stable isotopes such as oxygen and lithium, and all of these will play an increasing role in developing our geological understanding. As demonstrated so convincingly by the Nd results (Champion & Cassidy 2007; Wyche et al. 2012; Mole et al. 2013), patterns in the geochronological data, possibly combined with geochemistry and geophysics datasets, have the potential to elucidate the history of the Archean cratons and identify the oldest fragments of the Earth's crust, and to resolve their evolution in space and time.

CONCLUSIONS

In this brief review, we have followed the emergence of geochronology as a key discipline in our understanding of the Archean geology of Western Australia, from the early pioneering efforts of Jeffery and his group at UWA in the 1950s to the highly efficient field-integrated program of SHRIMP-based U-Pb zircon dating currently undertaken by GSWA. Since the 1950s there have been immense changes in the instrumentation and techniques applied to geochronology and this technological evolution is continuing today with new developments in mass spectrometry, micro-crystallography, and laser and ion microprobes. The development of new instrumentation has been accompanied by the evolution of ideas and applications of geochronological systems. The great breakthrough in the development of Rb-Sr whole-rock dating in the 1950s has now been superseded by the application of U-Pb zircon geochronology in the 1990s.

In Australia at least, TIMS geochronology was largely supplanted by the expansion of SHRIMP-based dating in the 1980s and 90s. This has removed the need for highly demanding isotope dilution chemistry and opened up geochronology to all geologists, whereas before, the demands of the technology required that many exponents were analytically trained physicists and chemists. However, isotope-dilution TIMS remains an essential complement to micro-analytical methods, and is still the best technique for high-precision analysis of homogeneous minerals.

It is fair to say that the value of geochronology in solving problems of Archean correlations, in elucidating crustal evolution, and in placing mineral systems in tectonic settings, was not well appreciated by government and industry geologists up until the 1980s, except by a few outstanding individuals such as Alan Wilson and Alec Trendall. This has now changed and we look forward to new developments in technology and new ideas in the application of geochronology and isotope geology to problems of Archean geology in Western Australia in the years to come.

ACKNOWLEDGEMENTS

We thank William Compston, Ian Fletcher, Arthur Hickman, Chris Kirkland, Malcolm McCulloch, Neal McNaughton and Stephen Wyche for helpful discussions on the history of research into the Archean of Western Australia. We also thank Simon Wilde for a very constructive review. Robert Pidgeon acknowledges research support from Curtin Research and Development. Michael Wingate publishes with permission of the Executive Director of the Geological Survey of Western Australia.

REFERENCES

- ALDRICH L T, DOAK J B & DAVIS G L 1953. The use of ion exchange columns in mineral analysis of age determination. *American Journal of Science* **251**, 377–387.
- Amelin Y V 1998. Geochronology of the Jack Hills detrital zircons by precise U–Pb isotope dilution analysis of crystal fragments. *Chemical Geology* **146**. 25–38.
- AMELIN Y V & DAVIS W J 2006. Isotopic analysis of lead in subnanogram quantities by TIMS using a ²⁰²Pb–²⁰⁵Pb spike. Journal of Analytical and Atomic Spectrometry, 21: 1063–1061.
- AMELIN Y V, LEE D-C, HALLIDAY A N & PIDGEON R T 1999. Nature of the Earth's earliest crust from hafnium isotopes in single detrital zircons. *Nature* 399, 252–255.
- Arriens P A 1971. The Archaean geochronology of Australia. *In:*Glover J E (ed.) *Symposium on Archaean rocks*, pp. 11–23.
 Geological Society of Australia Special Publication 3.
- BARLEY M E & DE LAETER J R 1984. Disturbed Rb-Sr whole-rock systems of the early Archaean Duffer Formation, Eastern Pilbara Block, Western Australia. *Journal of the Royal Society* of Western Australia 66, 129–134.
- BICKLE M J, BETTENAY L F, CHAPMAN H J, GROVES D I, MCNAUGHTON N J, CAMPBELL I H & DE LAETER J R 1989. The age and origin of younger granitic plutons of the Shaw Batholith in the Archaean Pilbara Block, Western Australia. Contributions to Mineralogy and Petrology 101, 361–376.
- BICKLE M J, BETTENAY L F, CHAPMAN H J, GROVES D I, McNaughton N J, Campbell I H & De Laeter J R 1993. Origin of the 3500 Ma 3300 Ma calc-alkaline rocks in the Pilbara Archaean: isotopic and geochemical constraints. *Precambrian Research* 60, 117–149.
- BLICHERT-TOFT J & ALBARÉDE F 2008. Hafnium isotopes in Jack Hills zircon and the formation of the Hadean Crust. Earth and Planetary Science Letters 265, 686–702.
- Bosch D, Bruguer O & Pidgeon R T 1996. Evolution of an Archaean metamorphic belt: a conventional and SHRIMP U—Pb study of accessory minerals from the Jimperding metamorphic belt, Yilgarn Craton, Western Australia. *Journal of Geology* 104, 695–711.
- Buick R, Thornet J R, McNaughton N J, Smith J B, Barley M E & Savage M 1995. Record of emergent continental crust ~3.5

- billion years ago in the Pilbara Craton of Australia. *Nature* **375**, 574–577.
- BYERLY G R, LOWE D R, WOODEN J L & XIE X 2002. An Archean impact layer from the Pilbara and Kaapvaal cratons. *Science* 297, 1325–1327.
- Cassidy K, Champion D, Krapež B, Barley M E, Brown S J A, Blewett R S, Groenewald P B & Tyler I M 2006. A revised geological framework for the Yilgarn Craton, Western Australia. Geological Survey of Western Australia Record 2006/8.
- CAVOSIE A J, VALLEY J W & WILDE S A 2005. Magmatic δ^{IS}O in 4400–3900 Ma detrital zircons: a record of the alteration and recycling of crust in the Early Archean. Earth and Planetary Science Letters 235, 663–681.
- Champion D C & Cassidy K F 2007. An overview of the Yilgarn Craton and its crustal evolution. *In:* Bierlein F P & Knox-Robinson C M (eds) *Proceedings of Geoconferences (WA) Inc. Kalgoorlie '07 Conference, 25–27 September 2007, Kalgoorlie Western Australia*, pp.8–13. Geoscience Australia Record 2007/14.
- CLEMENT S W J, COMPSTON W & NEWSTEAD G 1977. Design of a large high resolution ion microprobe. *In: Abstract volume of 1st International Conference on Secondary ion Mass Spectrometry, Münster* (published in full as Appendix 1 of Ireland *et al.* 2008).
- CLAOUÉ-LONG J C, COMPSTON W & COWDEN A 1988. The age of the Kambalda greenstones resolved by ion-microprobe: implications for Archaean dating methods. *Earth and Planetary Science Letters* 89, 239–259.
- CLAOUÈ-LONG J C, THIRLWALL M F & NESBITT R W 1984. Revised Sm-Nd systematics of Kambalda greenstones, Western Australia. *Nature* 307, 697–701.
- COMPSTON W & JEFFERY P M 1959. Anomalous "Common Strontium" in granite. Nature 184, 1792–1793.
- Compston W, Jeffery P M & RILEY G H 1960. Age of emplacement of granite. *Nature* 186, 702–703.
- COMPSTON W & ARRIENS P A 1968. The Precambrian geochronology of Australia. Canadian Journal of Earth Sciences 5, 561–583.
- Compston W & Pidgeon R T 1986. Jack Hills, evidence of more very old detrital zircons in Western Australia. *Nature* 321, 766–769.
- Crowley J L, Myers J S, Sylvester P J & Cox R A 2005. Detrital zircon from the Jack Hills and Mount Narryer, Western Australia: evidence for diverse >4.0 Ga source rocks. *Journal of Geology* 113, 239–263.
- De Laeter J R 1994. A question of time: Royal Society Medallist's Lecture for 1993. Journal of the Royal Society of Western Australia 77, 5–14.
- De Laeter J R & Baxter J L 1987. Rb-Sr geochronology of granitoids from Mount Mulgine, Western Australia. *Journal of the Royal Society of Western Australia* 69, 113–116.
- De Laeter J R & Blockley J G 1972. Granite ages within the Archean Pilbara Block. *Journal of the Geological Society of Australia* 19, 363–370.
- De Laeter J R, Fletcher I R, Bickle M J, Myers J S, Libby W G & Williams I R 1985. Rb–Sr, Sm–Nd and Pb–Pb geochronology of the ancient gneisses from Mount Narryer, Western Australia. *Australian Journal of Earth Sciences* 32, 349–358.
- De Laeter J R, Fletcher I R, Rosman K J R, Williams I R, Gee R D. & Libby W G 1981a. Early Archaean gneisses from the Yilgarn Block, Western Australia. *Nature* 292, 322–324.
- De Laeter J R & Kennedy A K 1998. A double focusing mass spectrometer for geochronology. *International Journal of Mass Spectrometry* 178, 43–50.
- De Laeter J R, Lewis J D & Blockley J G 1975. Granite ages within the Shaw Batholith of the Pilbara Block. Geological Survey of Western Australia Annual Report for 1974, 73–79.
- De Laeter J R, Libby W G & Trendall A F 1981b. The older Precambrian geochronology of Western Australia. *In*: Glover

- J E & Groves D I (eds) *Archaean geology: Proceedings Second International Symposium, Perth* 1980, pp. 145–157. Geological Society of Australia Special Publication 7.
- De Laeter J R & Martyn J E 1986. Age of the molybdenumcopper mineralization at Coppin Gap, Western Australia. Australian Journal of Earth Sciences 33, 65–71.
- DE LAETER J R & TRENDALL A F 1970. The age of the Copper Hills porphyry. Geological Survey of Western Australia Annual Report for 1969, 54–59.
- De Laeter J R & Trendall A F 1979. The contribution of geochronology to Precambrian studies of Western Australia. *Journal of the Royal Society of Western Australia* 62, 21–31.
- DE LAETER J R & TRENDALL A F 2002. The oldest rocks: the Western Australian connection. Journal of the Royal Society of Western Australia 85, 153–160.
- Dunn S J, Nemchin A A, Cawood P A & Pidgeon R T 2005. Provenance record of the Jack Hills metasedimentary belt: source of the Earth's oldest zircons. *Precambrian Research* 138, 235–254.
- Dunphy J M, Fletcher I R, Cassidy K E & Champion D C 2003. Compilation of SHRIMP U-Pb geochronology data, Yilgarn Craton, Western Australia, 2001–2002. *Geoscience Australia Record* 2003/15.
- FLETCHER I R, DUNPHY J M, CASSIDY K F & CHAMPION D C 2001. Compilation of SHRIMP U-Pb geochronological data, Yilgarn Craton, Western Australia, 2000–2001. Geoscience Australia Record 2001/47.
- FLETCHER I R & MCNAUGHTON N J 2002. Granitoid geochronology: SHRIMP zircon and titanite data. In: Cassidy K E, Champion D C, McNaughton N J, Fletcher I R, Whitaker A, Bastrakova I & Budd A R (eds) Characterisation and metallogenic significance of Archaean Granitoids of the Yilgarn Craton, Western Australia, pp. 6-1-6.156. Minerals and Energy Research Institute of Western Australia Report P482.
- FLETCHER I R & ROSMAN K J R 1984. Sm-Nd geochronology of greenstone belts in the Yilgarn Block, Western Australia. *Precambrian Research* 26, 333–361.
- FLETCHER I R, ROSMAN K J R & LIBBY W G 1988. Sm-Nd, Pb-Pb and Rb-Sr geochronology of the Manfred Complex, Mount Narryer, Western Australia. *Precambrian Research* 38, 343–354.
- FLETCHER I R, WILDE S A & ROSMAN K J R 1985. Sm-Nd model ages across the margins of the Archaean Yilgarn Block, eastern Australia III. The western margin. Australian Journal of Earth Sciences 32, 73-82.
- FLETCHER I R, WILLIAMS S J, GEE R D & ROSMAN K J R 1983. Sm—Nd model ages across the margins of the Archaean Yilgarn Block, Western Australia; northwest transect into the Proterozoic Gascoyne Province. Journal of the Geological Society of Australia 30, 167–174.
- Froude D O, Ireland T R, Kinny P D, Williams I S, Compston W, Williams I R & Myers J S 1983. Ion microprobe identification of 4100–4200 Myr-old terrestrial zircons. *Nature* 304, 616–618.
- GLIKSON A Y, ALLEN C & VICKERS J 2004. Multiple 3.47-Ga-old asteroid impact fallout units, Pilbara Craton, Western Australia. Earth and Planetary Science Letters 221, 383–396.
- Greenhalgh D & Jeffery P M 1959. A contribution to the pre-Cambrian chronology of Australia. *Geochimica et Cosmochimica Acta* 16, 39–57
- HAMILTON P J, EVENSON N M, O'NIONS R K, SMITH H S & ERLANK A J 1979. Sm-Nd dating of Onverwacht Group Volcanics, southern Africa. Nature 279, 298–300.
- HARRISON T M, BLICHERT-TOFT J, MULLER W, ALBARÉDE F, HOLDEN P & MOJZSIS S J 2005. Heterogeneous Hadean hafnium: evidence of continental crust at 4.4 to 4.5 Ga. Science 310, 1947–1950.
- HICKMAN A H 1981. Crustal evolution of the Pilbara Block, Western Australia. In: Glover J E & Groves D I (eds) Archaean geology: Proceedings Second International Symposium, Perth 1980, pp. 57–69. Geological Society of Australia Special Publication 7.

- HICKMAN A H 1983. Geology of the Pilbara Block and its environs. Geological Survey of Western Australia Bulletin 127.
- HICKMAN A H & LIPPLE S L 1975. Explanatory Notes on the Marble Bar 1:250 000 Geological Sheet, Western Australia. Geological Survey of Western Australia Record 1974/20.
- HICKMAN A H & SMITHES R H in prep. Archean geology of the northwest Pilbara Craton, Western Australia. Geological Survey of Western Australia Report 92.
- HICKMAN A H & VAN KRANENDONK M J 2012a. Early Earth evolution: evidence from the 3.5–1.8 Ga geological history of the Pilbara region of Western Australia. *Episodes* 35, 283–297.
- HICKMAN A H & VAN KRANENDONK M J 2012b. A billion years of Earth history: a geological transect through the Pilbara Craton and the Mount Bruce Supergroup — a field guide to accompany 34th IGC Excursion WA-2. Geological Survey of Western Australia Record 2012/10.
- HORWITZ R & PIDGEON R T 1993, 3.1 Ga tuff from the Sholl Belt in the west Pilbara: further evidence for diachronous volcanism in the Pilbara Craton of Western Australia. *Precambrian Research* 60, 175–183.
- IRELAND T R, CLEMENT S, COMPSTON W, FOSTER J J, HOLDEN P, JENKINS B, LANC P, SCHRAM N & WILLIAMS 1 S 2008. Development of SHRIMP. Australian Journal of Earth Sciences 55, 937–954.
- IVANIC T J, WINGATE M T D, KIRKLAND C L, VAN KRANENDONK M J & WYCHE S 2010. Age and significance of voluminous 2815– 2715 Ma layered mafic-ultramafic intrusions in the Murchison Domain, Yilgarn Craton. Australian Journal of Earth Sciences 57, 597–614.
- Kemp A I S, Wilde S A, Hawkesworth C J, Coath C D, Nemchin A A & Pidgeon R T 2010. Hadean crustal evolution revisited: new constraints from Pb-Hf systematics of the Jack Hills zircons. Earth and Planetary Science Letters 296, 45–56.
- KINNY P D 1990. Age spectrum of detrital zircons in the Windmill Hill Quartzite. In: Ho S E, Glover J E, Myers J S & Muhling J R (eds) 3rd International Archaeau symposium, Excursion Guide Book, pp. 116–117. Geology Department and University Extension, University of Western Australia Publication 21.
- KINNY P D & NUTMAN A P 1996. Zirconology of the Meeberrie Gneiss, Yilgarn Craton, Western Australia: an early Archaean migmatite. *Precambrian Research* 78, 165–178.
- KINNY P D, WILLIAMS I S, FROUDE D O, IRELAND T R & COMPSTON W 1988. Early Archaean zircon ages from orthogneiss and anorthosites at Mount Narryer, Western Australia. *Precambrian Research* 38, 325–341.
- Kirkland C L, Spaggiari C V, Wingate M T D, Smithies R H, Belousova E A, Murphy R & Pawley M J 2011. Inferences on crust–mantle interaction from Lu–Hf isotopes: a case study from the Albany–Fraser Orogen. *Geological Survey of Western Australia Record* 2011/12.
- KIRKLAND C L & WINGATE M T D 2013. Reading deep time: radiogenic isotope geochronology. Geological Survey of Western Australia Record 2012/15.
- Kosticin N, Brown S J A, Barley M E, Krapez B, Cassidy K F & Champion D C 2008. SHRIMP U-Pb zircon age constraints on the Late Archaean tectonostratigraphic architecture of the Eastern Goldfields Superterrane, Yilgarn Craton, Western Australia. *Precambrian Research* 161, 5–33.
- KOBER B, PEDGEON R T & LIPPOLT H J 1989. Single-zircon dating by stepwise Pb-evaporation determines the Archaean history of detrital zircons from the Jack Hills, Western Australia. Earth and Planetary Science Letters 91, 286–296.
- Leggo P J, Compston W & Trendall A F 1965. Radiometric ages of some Precambrian rocks from the Northwest Division of Western Australia. *Journal of the Geological Society of Australia* 12, 53–65.
- Lowe D R & Byerly G R 1986. Early Archean silicate spherules of probable impact origin, South Africa and Western Australia, *Geology* 14, 83–86.

- MAAS R & MCCULLOCH M T 1991. The provenance of Archaean clastic metasediments in the Narryer Gneiss Complex, Western Australia: trace element geochemistry, Nd isotopes, and U-Pb ages for detrital zircons. *Geochimica et Cosmochimica Acta* 55, 1914–1932.
- McCulloch M T & Compston W 1981. Sm-Nd age of Kambalda and Kanowna greenstones and heterogeneity in the Archaean mantle. *Nature* 294, 322–327.
- McCulloch M T, Collerson K D & Compston W 1983b. Growth of Archaean crust within the Yilgarn Block, Western Australia. *Journal of the Geological Society of Australia* 30, 155–160.
- McCulloch M T, Compston W & Froude D 1983a. Sm-Nd and Rb-Sr dating of Archaean gneisses, Eastern Yilgarn Block, Western Australia. *Journal of the Geological Society of Australia* 30, 149–153.
- McNaughton N J & Bickle M J 1987. K-feldspar Pb-Pb isotope systematics of Archaean post-kinematic granitoid intrusions of the Diemals area, central Yilgarn Block. *Chemical Geology* 66, 193–208.
- McNaughton N J & Cassidy K F 1990. The age of the Liberty Granodiorite: a reassessment of the broad synchroneity of mesothermal gold mineralization within the Norseman— Wiluna Belt, Western Australia. Australian Journal of Earth Sciences 37, 373–376.
- McNaughton N J, Green M D, Compston W & Williams I S 1988. Are anorthositic rocks basement to the Pilbara Craton? Geological Society of Australia Abstracts 21: 272–273.
- McNaughton N J & Groves D I 1996. A review of Pb-isotope constraints on the genesis of lode-gold deposits in the Yilgarn Craton, Western Australia. *Journal of the Royal Society of Western Australia* 79, 123–129.
- MOJZSIS S J, HARRISON T M & PIDGEON R T 2001. Oxygen-isotope evidence from ancient zircons for liquid water at the Earth's surface 4300 Ma ago. *Nature* 409, 178–181.
- MOLE D R, FIORENTINI M L, THEBAUD N, MCCUAIG T C, CASSIDY K F, KIRKLAND C L, WINGATE M T D, ROMANO S S, DOUBLIER M P & BELOUSOVA E A 2012. Spatio-temporal constraints on lithospheric development in the southwest-central Yilgarn Craton, Western Australia. *Australian Journal of Earth Sciences* 59, 625–656.
- Mole D R, Fiorentini M L, Cassidy K F, Kirkland C L, Thebaud N, McCuaig T C, Doublier M P, Duuring P, Romano S S, Maas R, Belousova E A, Barnes S J & Miller J 2013. Crustal evolution, intra-cratonic architecture and the metallogeny of an Archaean craton. *In:* Jenkin G R T, Lusty P A J, McDonald I, Smith M P, Boyce A J & Wilkinson J J (eds) *Ore deposits in an evolving Earth*. Geological Society of London Special Publication 393. doi:10.1144/SP393.8
- MUHLING P C & DE LAETER J R 1971. Ages of granitic rocks in the Poona–Dalgaranga area of the Yilgarn Block, Western Australia. *In:* Glover J E (ed.) *Symposium on Archaean rocks*, pp. 25–31. Geological Society of Australia Special Publication 3.
- MYERS J S & WILLIAMS 1 R 1985. Early Precambrian crustal evolution at Mount Narryer, Western Australia. *Precambrian* Research 27, 153–163.
- Nelson D R 1995. Compilation of SHRIMP U-Pb zircon geochronology data, 1994. Geological Survey of Western Australia Record 1995/3.
- NELSON D R 1996. 105007: leucocratic orthogneiss, Churla Well. Geological Survey of Western Australia Geochronology Record 12.
- Nelson D R 1997a. Compilation of SHRIMP U-Pb zircon geochronology data, 1996. Geological Survey of Western Australia Record 1997/2.
- Nelson D R 1997b. Evolution of the Archaean granitegreenstone terranes of the Eastern Goldfields, Western Australia: SHRIMP U-Pb zircon constraints. *Precambrian* Research 83, 57-81.
- Nelson D R 1997c. 105007: leucocratic orthogneiss, Churla Well. Geological Survey of Western Australia Geochronology Record 13.

- Nelson D R 2005. 178064: coarse sandstone, The Stock Well. Geological Survey of Western Australia Geochronology Record 591.
- Nelson D R, Robinson B W & Myers J S 2000. Complex geological histories extending for ≥ 4.0 Ga deciphered from xenocryst zircon microstructures. *Earth and Planetary Science Letters* 181, 89–102.
- Nemchin A A & Pidgeon R T 1997. Evolution of the Darling Range Batholith, Yilgarn Craton, Western Australia: a SHRIMP zircon study. *Journal of Petrology* 38, 625–649.
- NIEUWLAND D A & COMPSTON W 1981. Crustal evolution in the Yilgarn Block near Perth, Western Australia. In: Glover J E & Groves D 1 (eds) Archaean geology: Proceedings Second International Symposium, Perth 1980, pp. 159–171. Geological Society of Australia Special Publication 7.
- NUTMAN A P, BENNETT V C, KINNY P D & PRICE R 1993. Largescale crustal structure of the Northwestern Yilgarn Craton, Western Australia: evidence from Nd isotopic data and zircon geochronology. *Tectonics* 12, 971–981.
- Nutman A P, Kinny P D, Compston W & Williams I S 1991. SHRIMP U-Pb zircon geochronology of the Narryer Gneiss Complex, Western Australia. *Precambrian Research* 52, 275–300.
- Oversby V M 1975. Lead isotope systematics and ages of Archaean acid intrusives in the Kalgoorlie–Norsemen area, Western Australia. *Geochimica et Cosmochimica Acta* 39, 1107– 1125.
- Oversby V M 1976. Isotopic ages and geochemistry of Archaean acid igneous rocks from the Pilbara, Western Australia. Geochimica et Cosmochimica Acta 40, 817–829.
- Pawley M J, Wingate M T D, Kirkland C L, Wyche S, Hall C E, Romano S S & Doublier M P 2012. Adding pieces to the puzzle: episodic crustal growth and a new terrane in the northeast Yilgarn Craton, Western Australia. Australian Journal of Earth Sciences 59, 603–623.
- PECK W H, VALLEY J W, WILDE S A & GRAHAM C M 2001. Oxygen isotope ratios and rare earth elements in 3.3 to 4.4 Ga zircons: ion microprobe evidence for high δ¹⁸O continental crust and oceans in the Early Archean. Geochimica et Cosmochimica Acta 65, 4215–4229.
- Perring C S & McNaughton N J 1990. Proterozoic remobilization of ore metals within Archaean gold deposits: lead isotope evidence from Norseman, Western Australia. *Australian Journal of Earth Sciences* 37, 369–372.
- Perring C S & McNaughton N J 1992. The relationship between Archaean gold mineralization and spatially associated minor intrusives at the Kambalda and Norseman gold camps, Western Australia: lead isotope evidence. *Mineralium Deposita* 27, 10–22.
- Pidgeon R T 1978a. 3450 M.Y. old volcanics in the Archaean layered greenstone succession of the Pilbara Block, Western Australia. *Earth and Planetary Science Letters* 37, 421–428.
- Pidgeon R T 1978b. Geochronological investigation of granite batholiths of the Archaean granite–greenstone terrain of the Pilbara Block, Western Australia. *In:* Smith 1 E M & Williams J G (eds) *Proceedings of the 1978 Archaean Geochemistry Conference*, pp. 360–362. University Toronto Press, Toronto.
- PIDGEON R T 1984. Geochronological constraints on early volcanic evolution of the Pilbara Block, Western Australia. Australian Journal of Earth Sciences 31, 237–242.
- PIDGEON R T & HALLBERG J A 2000. Age relationships in supracrustal sequences in the northern part of the Murchison Terrane, Archaean Yilgarn Craton, Western Australia: a combined field and zircon U-Pb study. Australian Journal of Earth Sciences 47, 153–165.
- PIDGEON R T & NEMCHIN A A 2006. High abundance of early Archaean grains and the age distribution of detrital zircons in a sillimanite-bearing quartzite from Mount Narryer, Western Australia. *Precambrian Research* 150, 201–220.
- Pidgeon R T & Wilde S A 1990. The distribution of 3.0 and 2.7 Ga volcanic episodes in the Yilgarn Craton of Western Australia. *Precambrian Research* 48, 309–325.

- Pidgeon R T & Wilde S A 1998. The interpretation of complex zircon U-Pb systems in Archaean granitoids and gneisses from the Jack Hills, Narryer Gneiss Terrane, Western Australia. *Precambrian Research* 91, 309–332.
- PIDGEON R T, WILDE S A, COMPSTON W & SHIELD M W 1990. Archaean evolution of the Wongan Hills Greenstone Belt, Yilgarn Craton, Western Australia. *Australian Journal of Earth Sciences* 37, 279–292.
- Pidgeon R T, Wingate M T D, Bodorkos S & Nelson D R 2010. The age distribution of detrital zircons in quartzites from the Toodyay-Lake Grace Domain, Western Australia: implications for the early evolution of the Yilgarn Craton. *American Journal of Science* 310, 1115–1135.
- RICHARDS J R, FLETCHER I R & BLOCKLEY J G 1981. Pilbara galenas: precise isotopic assay of the oldest Australian leads; model ages and growth-curve implications. *Mineralium Deposita* 16, 7–30.
- RODDICK J C 1984. Emplacement and metamorphism of Archaean mafic volcanics at Kambalda, Western Australia – geochemical and isotopic constraints. *Geochimica et Cosmochimica Acta* 48, 1305–1318.
- Sangster D F & Brook W A 1977. Primitive lead in an Australian Zn-Pb-Ba deposit. *Nature* 270, 423.
- SCHÄRER U & ALLEGRE C J 1985. Determination of the age of the Australian continent by single grain analysis of Mount Narryer metaquartzite. *Nature* 315, 52–55.
- SCHIØTTE L & CAMPBELL I H 1996. Chronology of Mount Magnet granite-greenstone terrain, Yilgarn Craton, Western Australia: implications for field based predictions of the relative timing of granitoid emplacement. *Precambrian Research* 78, 237–260.
- SIRCOMBE K N, CASSIDY K F, CHAMPION D C & TRIPP G 2007. Compilation of SHRIMP U-Pb geochronological data, Yilgarn Craton, Western Australia, 2004–2006. Geoscience Australia Record 2007/01.
- STACEY J S & KRAMERS J D 1975. Approximation of terrestrial lead isotope evolution by a two stage model. Earth and Planetary Science Letters 26, 207–221.
- THERN R E & NELSON D R 2012. Detrital zircon age structure within ca. 3 Ga metasedimentary rocks, Yilgarn Craton: elucidation of Hadean source terranes by principal component analysis. *Precambrian Research* 214, 28–43.
- THORPE R I, HICKMAN A H, DAVIS D W, MORTENSEN J K & TRENDALL A F 1992. U-Pb zircon geochronology of Archaean felsic units in the Marble Bar region, Pilbara Craton, Western Australia. *Precambrian Research* 56, 169–189.
- TILTON G R, PATTERSON C, BROWN H, INGLIRAM M, HAYDEN R, HESS D & LARSEN E 1955. Isotopic composition and distribution of lead, uranium and thorium in a Precambrian granite. *Bulletin of the Geological Society of America* 66, 1131–1148.
- Trendall A F & Blockley J D 2004. Precambrian iron-formations. In: Erikson P G, Altermann W, Nelson D R, Mueller W U & Catuneanu O (eds) The Precambrian Earth: tempos and events in Precambrian time (Developments in Precambrian Geology 12), pp. 403–421. Elsevier, Amsterdam.
- Trendall A F, Nelson D R, De Laeter J R. & Hassler S W 1998. Precise zircon U-Pb ages from the Marra Mamba Iron Formation and the Wittenoom Formation, Hamersley Group, Western Australia. Australian Journal of Earth Sciences 45, 137–142.
- Turek A 1966. Rubidium–strontium isotopic studies in the Kalgoorlie–Norseman area, Western Australia. PhD thesis, Australian National University, Canberra (unpubl.).
- Valley J W, PFCK W H, KING E M & WILDE S A 2002. A cool early Earth. Geology 30, 351–354.
- VAN KRANENDONK M J, IVANIC T J, WYCHE S, WILDE S A & ZIBRA I 2010. A time transect through the Hadean to Neoarchean geology of the western Yilgarn Craton a field guide. Geological Survey of Western Australia Record 2010/19.

- VAN KRANENDONK M J, IVANIC T J, WINGATE M T D, KIRKLAND C L & WYCHE S 2013. Long-lived, autochthonous development of the Archean Murchison Domain, and implications for Yilgarn Craton tectonics. Precambrian Research 229, 49–92.
- Van Kranendonk M J, Philippot P, Lepot K, Bodorkos S & Pirajno F 2008. Geological setting of Earth's oldest fossils in the ca. 3.5 Ga Dresser Formation, Pilbara Craton, Western Australia. *Precambrian Research* 167, 93–124.
- Walter M R, Burck R & Dunlop J S R 1980. Stromatolites, 3,400–3,500 Myr old from the North Pole area, Western Australia. *Nature* 284, 443–445.
- WANG Q 1998. Geochronology of the granite-greenstone terranes in the Murchison and Southern Cross provinces of the Yilgarn Craton, Western Australia. PhD thesis, Australian National University, Canberra (unpubl.).
- WASSERBURG G J 1954. Argon40/potassium40 dating. In: Faul H (ed.) Nuclear Geology, pp. 341–349. Wiley and Sons, New York.
- WIEDENBECK M & WATKINS K P 1993. A time scale for granitoid emplacement in the Archaean Murchison Province, Western Australia, by single zircon geochronology. *Precambrian Research* 61, 1–26.
- WIJBRANS J R & McDougall I 1987. On the metamorphic history of an Archaean granitoid greenstone terrain, East Pilbara, Western Australia, using the 40 Ar/ 39 Ar age spectrum method. Earth and Planetary Science Letters 84, 226–242.
- WILDE S A & PIDGEON R T 1986. Geology and geochronology of the Saddleback Greenstone belt in the Archaean Yilgarn Block, southwestern Australia. *Australian Journal of Earth Sciences* 33, 491–501.
- WILDE S A & SPAGGIARI C V 2007. The Narryer Terrane, Western Australia: a review. In: Van Kranendonk M J, Smithies R H & Bennett V C (eds) Earth's oldest rocks (Developments in Precambrian Geology 15), pp. 275–304. Elsevier, Amsterdam.
- WILDE S A, VALLEY J W, PECK W H & GRAHAM C M 2001. Evidence from detrital zircons for the existence of continental crust and oceans on Earth 4.4 Gyr ago. Nature 409, 175–177.
- WILSON A F, COMPSTON W, JEFFERY P M & RILEY G H 1960. Radioactive ages from the Precambrian rocks in Australia. Journal of the Geological Society of Australia 6, 179–195.
- WILLIAMS I S & COLLINS W J 1990. Granite-greenstone terranes in the Pilbara Block, Western Australia, as coeval volcanicplutonic complexes: evidence from U-Pb zircon dating of the Mount Edgar Batholith. Earth and Planetary Science Letters 97, 41–53.
- Wingate M T D 1999. Ion microprobe baddeleyite and zircon ages for late Archean mafic dykes of the Pilbara Craton, Western Australia. Australian Journal of Earth Sciences 46, 493–500
- WINGATE M T D, BODORKOS S & VAN KRANENDONK, M J 2009. 180070: volcaniclastic sandstone, drillcore PDP2c, Dresser Mine. Geological Survey of Western Australia Geochronology Record 811
- WINGATE M T D, KIRKLAND C L, RIGANTI A & WYCHE S 2011. 185990: metagabbro, Grass Flat Bore. Geological Survey of Western Australia Geochronology Record 868.
- Wyche S, Nelson D R & Riganti A 2004. 4350–3130 Ma detrital zircons in the Southern Cross Granite–Greenstone Terrane, Western Australia: implications for the early evolution of the Yilgarn Craton. Australian Journal of Earth Sciences 51, 31–45.
- WYCHE S, KIRKLAND C L, RIGANTI A, PAWLEY M J, BELOUSOVA E & WINGATE M T D 2012. Isotopic constraints on stratigraphy in the central and eastern Yilgarn Craton, Western Australia. Australian Journal of Earth Sciences 59, 657–670.

Received 4 November 2013; accepted 16 January 2014



Early Paleozoic colonisation of the land: evidence from the Tumblagooda Sandstone, Southern Carnarvon Basin, Western Australia

K J McNAMARA

Department of Earth Sciences, University of Cambridge, Downing Street, Cambridge CB2 3EQ, UK. A kjm47@cam.ac.uk

The early Paleozoic Tumblagooda Sandstone outcrops principally in the vicinity of the Murchison River in Kalbarri National Park, Western Australia. It contains a great variety of trace fossils that provide a unique insight into the activities of early invaders of the terrestrial environment, and may record one of the earliest known freshwater and terrestrial ecosystems. The traces reveal that this nascent terrestrial fauna was dominated by arthropods. In outcrop the sandstones are more than 1 km thick and comprise predominantly mixed fluvial and eolian deposits. The age of the Tumblagooda Sandstone has been the subject of much debate. Initial analysis of the trace-fossil assemblage suggested a Late Silurian age. Preliminary work on conodont faunas in sediments of the conformably overlying Dirk Hartog Group also indicated a Silurian age. However, arguments have been made for an older, Ordovician age based on paleomagnetic and pedostratigraphic studies. In this review it is argued that deposition is linked to the known ages of regional uplift of the hinterland, and thus inferred to be Early to mid-Silurian. A previous study recognised two distinct trace-fossil assemblages. One, comprising a mixture of burrows and arthropod trackways, represents a freshwater/terrestrial ecosystem that inhabited sands interpreted as having been deposited in broad, low sinuosity, braided fluvial channels, between mixed eolian and water-lain sandsheets, small eolian dunes and flooded interdune, and deflation hollows. The major bioturbator was Heimdallia. Other burrows include Tumblagoodichnus, Beaconites and Diplocraterion. A variety of arthropod trackways, predominantly Diplichnites, formed on water-lain sands and foreset beds of eolian dunes. Other tracks include Siskemia and possible examples of Paleolelcura and Protichuites. Other arthropod traces include Rusophycus and Cruziana. Likely arthropod track makers include myriapods, eurypterids, euthycarcinoids and xiphosurids. A single trackway is interpreted as having been made by a tetrapod and as such pushes back the record of this group from the mid-Devonian to the Early-mid-Silurian. This trace fossil assemblage can be assigned to the Scoyenia ichnofacies. A second trace fossil assemblage, assignable to the Skolithos ichnofacies occurs higher in the section, in strata traditionally interpreted as having been deposited in a marginal fluvial-marine environment. The ichnofacies is dominated by burrows, especially Skolithos, but also Diplocraterion, Daedalus and Lunatubichnus. Rare locomotory traces are assignable to Diplichuites and Aulichnites. Preservation of the arthropod trackways in the Scoyenia ichnofacies was facilitated by the nature of the fluvial/eolian environment. Many of the tracks show indication of having been created subacrially on wet sand surfaces, and preserved by a covering of fine, colian sand. The presence of extensive dwelling burrows and terrestrial trackways in the Scoyenia ichnofacies represents arguably the earliest known freshwater/terrestrial ecosystem. Moreover, it supports the view that one of the major steps in evolution, the colonisation of land by animals, may have been from rivers, rather than directly from the sea.

KEYWORDS: arthropods, Paleozoic, terrestrialisation, tetrapods, trace fossils.

INTRODUCTION

Covering an area of more than 7000 km² on the western margin of the Precambrian Yilgarn Craton, the early Paleozoic Tumblagooda Sandstone straddles both the Southern Carnarvon and Perth Basins. Although its actual age is the subject of much debate (see below), this thick sequence of sandstones remains the earliest known Phanerozoic deposits preserved in these marginal sedimentary basins. lasky *et al.* (1998) pointed out that seismic data indicate that the Tumblagooda Sandstone is about 3500 m thick in the southern part of the Gascoyne Platform, a sub-basin in the Southern Carnarvon Basin. The unit thins significantly to the north, away from the sediment source. The Southern Carnarvon Basin itself was an interior-fracture basin that opened to the north and formed as a consequence of rifting along the western

margin of the Yilgarn Craton (Hocking & Mory 2006). As such, the Tumblagooda Sandstone records the first sedimentological evidence for the initiation of this rifting along the western Australia margin during the early Paleozoic.

The Tumblagooda Sandstone is dominated by iron oxide-rich quartz arenites that have variously been interpreted as having been deposited largely in a terrestrial setting, predominantly braided fluvial and eolian, with minor marginal marine input (Trewin 1993a, b) or in a mixed fluvial and tidal marine environment (Hocking 1991; 2000; Hocking et al. 1987). These different interpretations are discussed further below. These sediments were deposited over a very wide area that extended from at least 150 km south of Kalbarri into the northern part of the Perth Basin (Hocking & Mory 2006) to more than 700 km north, near Onslow (Evans et al. 2007). Although the upper and lower boundaries of the Tumblagooda Sandstone are not exposed in outcrop in

the Kalbarri region, in the subsurface the sandstones are known to be conformably overlain by shallow-water limestones and dolomites of the Silurian Dirk Hartog Group (Mory *et al.* 1998). The formation is seen to rest unconformably on Precambrian basement west of the Northampton Complex (Hocking 1991 p. 6, figure 4).

On the basis of the excellent exposures of the Tumblagooda Sandstone for some 70 km in the gorge of the Murchison River in Kalbarri National Park, and in the coastal gorges to the south of Kalbarri (Figure 1), Hocking (1991) subdivided the 1300 m of sedimentary rocks exposed in these areas into four discrete packages, which he termed Facies Associations 1 to 4. This subdivision has been accepted and utilised by all subsequent workers. While there is consensus that the earliest, Facies Association (FA)1 and third, FA3, represent braided fluvial deposition, there is debate on the environment of deposition of FA2, a more variable unit that is dominated by thin-bedded sandstones. The youngest package, FA4, is generally accepted to represent a marginal marine environment of deposition.

Some parts of the Tumblagooda Sandstone, typically FA2 and FA4, contain rich trace-fossil assemblages, with a high diversity of trackways and burrows in both facies associations, with tracks especially dominant in FA2 and burrows in FA4 (Trewin & McNamara 1995). There is ample evidence from the style of preservation of some of the trackways that these were made by animals, predominantly arthropods, out of water. As such, these early Paleozoic redbed sandstones contain some of the best evidence anywhere for the early colonisation of land by animals, while the presence of a variety of established dwelling burrows in FA2 may record the earliest evidence for the establishment of a freshwater ecosystem.

In addition to discussion on the interpretation of the

environments of deposition of the sandstones, there has been much debate concerning the age of the unit, with suggested ages ranging from Cambrian to Devonian. Given its importance in our understanding of the earliest terrestrial ecosystems, defining the age of these sediments is of paramount importance. In this review an alternative methodology is proposed for establishing the age of the Tumblagooda Sandstone. The only papers to date on the fauna of the Tumblagooda Sandstone are descriptions of the trace-fossil fauna by Öpik (1959) and Trewin & McNamara (1995), and description of the lone body fossil found in this unit (McNamara & Trewin 1993). In this paper I review the trace-fossil fauna, drawing particularly on the work of Trewin & McNamara (1995), and discuss the implications of the fauna in the context of it being one of the earliest freshwater ecosystems.

AGE OF THE TUMBLAGOODA SANDSTONE

Any attempts to establish a definitive age for the Tumblagooda Sandstone are constrained by the present inability to obtain radiometric dates other than from detrital zircons, and the lack of any body fossils that would enable a refined biostratigraphic age. The only body fossil found to date, a single specimen of the euthycarcinoid *Kalbarria brimmellae* (McNamara & Trewin 1993), provides no help in this regard (Figure 2). Neither does the extensive trace-fossil assemblage in the sandstones (Trewin & McNamara 1995), with the ichnofacies being representative only of particular early Paleozoic ecosystems and not being age-diagnostic. Attempts have been made to infer the age from reliable biostratigraphic data from overlying lithostratigraphic

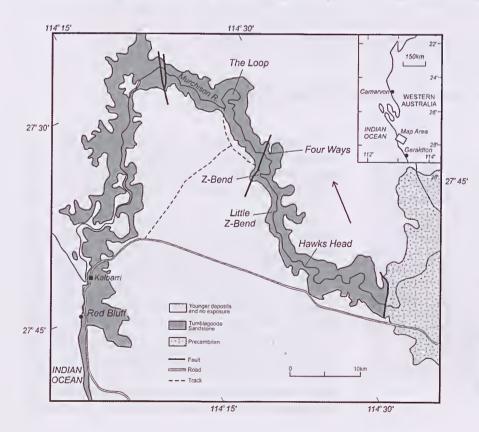


Figure 1 Map showing principal outcrops of the Tumblagooda Sandstone around the Murchison River (based on Trewin 1993a figure 1).



Figure 2 The euthycarcinoid *Kalbarria brimmellae* McNamara & Trewin 1993 from the Tumblagooda Sandstone. Holotype and only known specimen, WAM 90.158 from top of gorge at the eastern end of The Loop; FA2. Photo by K Brimmell.

units (Mory et al. 1998). However, even using this technique there are age discrepancies and they only provide a minimum age estimate.

The formations in the Dirk Hartog Group, which conformably overlies the Tumblagooda Sandstone in boreholes to the north of the main outcrops in the Murchison River area, have yielded conodont faunas. Philip (1969) interpreted these as indicating a Late Silurian (mid to late Ludlow) age, which implies the Tumblagooda Sandstone is earlier Silurian at the youngest. A minimum Silurian age is also suggested by conodonts that were obtained from the Dirk Hartog Group from mineral boreholes and stratigraphic wells. Six specimens from the Wandagee 1 well, located about 400 km north of Kalbarri, and first identified as Teridontus nakamurai by Gorter et al. (1994), were regarded as an undescribed species of Teridontus by Mory et al. (1998). As Mory et al. pointed out, this genus has a range of Late Cambrian to Early Ordovician and thus could be reworked, as all conodonts from elsewhere in the Dirk Hartog Group are Early Silurian or younger. They caution against using these elements as agediagnostic indicators. More reliable material was derived from the Dirk Hartog Group in other wells (Mory et al. 1998). The oldest of this material includes Ozarkodina broenlundi, a species that occurs within the

Pterospathognathus celloni zone, which is mid-Telychian (late Llandovery) in age (about 431 Ma: Ogg et al. 2008). The Tumblagooda Sandstone would thus be older.

A maximum age constraint is provided by a Pb mineralisation age of 434±16 Ma (Llandovery) obtained in the adjacent Northampton Inlier (Richards et al. 1985). There is no evidence of Pb mineralisation in the sandstones (Hocking 1991), indicating that mineralising fluids passed through the metamorphic rocks of the Northampton Inlier prior to the deposition of the Tumblagooda Sandstone. Byrne & Harris (1993) also observed that any models invoking post-Tumblagooda Sandstone mineralisation are not supportable by the evidence. However, Retallack (2009) stated that what he interpreted as gossans in the Tumblagooda Sandstone points to the influence of the mineralisation on the sandstones and a much older age for the formation. These were considered by Hocking (1991) to be simply relatively young ferruginous cementation of conglomeratic breccias by fluids leaking along fault planes, after gorge incision. No anomalous Pb values are known.

Despite this seeming relatively strong support for an Early Silurian age for the limestones that overlie the Tumblagooda Sandstone and a Silurian age because of the lack of mineralisation, other workers have suggested that there is further evidence for an older, pre-Silurian, age for the sandstone. Paleomagnetic studies of the Tumblagooda Sandstone favour an Ordovician age of deposition. A paleomagnetic reverse-to-normal transition was identified by Schmidt & Hamilton (1990) in the conglomeratic Gabba Gabba Member from FA4 in coastal outcrops south of Kalbarri and was correlated with the basal Silurian (444 Ma: Ogg et al. 2008), suggestive of a Late Ordovician age for the formation. Schmidt & Embleton (1990) further interpreted the position of the paleomagnetic pole at the time of deposition of the sediments. They argued that the paleomagnetic data do not support a Silurian pole position. They suggested, on the contrary, that the Tumblagooda Sandstone may therefore be anything from Cambrian to Ordovician in age. A recent outcrop gamma ray study of the Tumblagooda Sandstone assumed a Late Ordovician age (Evans et al. 2007).

More recently, Retallack (2009) claimed that paleosols are present in the Tumblagooda Sandstone, despite such features never having been seen previously by other workers. Both Hocking (1991) and Trewin (1993a, b), for instance, after undertaking exhaustive studies of the sedimentology of these sandstones, saw no evidence of soil-forming processes or paleosols. However, Retallack, working on the premise that depth of formation of nodular calcretes, which he claims he identified, is indicative of extent of levels of precipitation, interpreted 'pedostratigraphic spikes' in the Paleozoic across Australia. On the basis of this Retallack interpreted the Tumblagooda Sandstone as having been deposited over the entire Ordovician Period, a period of some 45 million years. Given the style of predominantly fluvial sedimentation in an environment when there was very little land vegetation cover (see below), it is extremely difficult to to see how this would have taken such an inordinately long period of time to be deposited.

None of these lines of evidence for the age of the Tumblagooda Sandstone are particularly rigorous. All

but the Pb mineralisation age of Richards *et al.* (1985) are compatible with or suggestive of a pre-Llandovery age, in other words it could be Early Silurian or Ordovician, or even earlier. An alternative strategy to establish the age of deposition of the Tumblagooda Sandstone is to look at the genesis of the sediments and ascertain whether the factors responsible for their accumulation can provide insights into their age of deposition.

A key feature of the Tumblagooda Sandstone is that it is the first known Phanerozoic deposition recorded in the Perth and Southern Carnarvon Basins, both of which lie to the west of the Precambrian Yilgarn Craton. As discussed below, the sandstones are a mixed sequence of predominantly sheet-braided fluvial sands (Hocking 1981, 2000; Trewin 1993a, b; Hocking & Mory 2006), and sandsheets, deposited either in a marine, tidal environment (Hocking 1979, 1981) or as eolian sandsheets and dunes (Trewin 1993a, b). Such a 'sheet-braided' style of siliciclastic sedimentation is characteristic of many early Paleozoic river systems due to the absence of an effective land vegetation up to this time (Cotter 1978; Hocking 1991; Davies & Gibling 2010).

Paleocurrent data from fluvial episodes in the Tumblagooda Sandstone indicate a general northwesterly trend of sediment transport (Hocking 1991; Trewin 1993a, b). Therefore onset of the fluvial sedimentation that characterises the Tumblagooda Sandstone must have been brought about by initiation of regional uplift to the southeast of its area of deposition (Hocking 1991 p. 22). Indication of a source of the sediments from the south also comes from an analysis of reworked zircons in the sandstones. These all suggest derivation not from nearby parts of the Yilgarn Craton to the east (Cawood & Nemchin 2000), but from the south, probably from the uplifted Prydz-Leeuwin Belt, from which the regional paleoslope produced a northward-flowing drainage system (Veevers et al. 2005). As noted by lasky et al. (1998), the sediments are correspondingly much thicker in the south.

Evidence for the timing of uplift of these southern terrains that provided the sediment comes from the ages of reheating of the biotites. Libby & De Laeter (1998) showed that erosional rebound following collision of the Australo-Antarctic and Indian–Antarctic domains resulted in biotite Rb/Sr dates being reset at about 430 Ma when the western margin of the Yilgarn Craton and the Albany Mobile Belt moved through the 320° isotherm. Further support for a period of uplift during the mid-Silurian comes from Nemchin & Pigeon (1999) who used U–Pb systems of apatites from granites from the western part of the Darling Range Batholith to show that there was a disturbance at about 420 Ma, suggestive of heating and uplift along the western margin of the craton.

These lines of evidence point to deposition of the Tumblagooda Sandstone during the Silurian, probably during the Llandovery. Of these, Pb mineralisation at 434±16 Ma in the nearby Northampton Inlier and not in the Tumblagooda Sandstone, provides a maximum age constraint. Secondly, conodonts in the overlying Dirk Hartog Limestone have a maximum age of late Llandovery (about 431 Ma). Lastly, there is the Rb/Sr biotite date of about 430 Ma resulting from heating associated with uplift that may have led to the production of the Tumblagooda Sandstone sediments.

TUMBLAGOODA SANDSTONE DEPOSITIONAL ENVIRONMENT

Major depositional cycles

Two significant sedimentary cycles have been recognised in the Tumblagooda Sandstone (Hocking 1991; Trewin 1993a, b). The first cycle consists of thick fluvial deposits (FA1) overlain by finer, but still sand-dominated, deposits (FA2) interpreted as mixed wholly freshwater, eolian and fluvial facies (FA2) (Figure 3) (Trewin 1993a, b; Trewin & McNamara 1995) or as marginal marine, tidally dominated facies (Hocking 1991, 2000). The sediments of FA1 are predominantly trough cross-bedded medium- to coarsegrained sandstones. As indicated, paleocurrent data

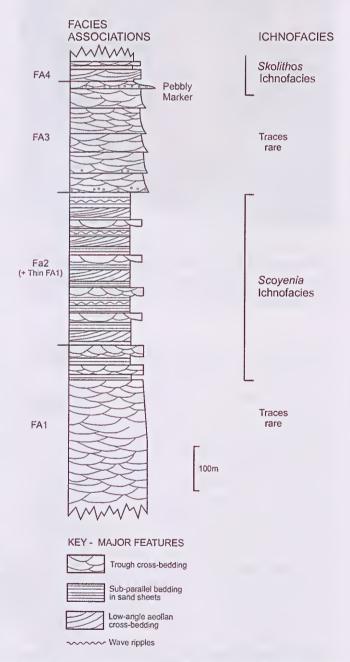


Figure 3 Composite diagrammatic section showing lithofacies and corresponding ichnofacies in the Tumblagooda Sandstone (based on Trewin 1993a figure 2, utilising data from Hocking 1979, 1981).

suggest a northwestward direction of transport, the sands having been deposited in large sheet-braided lobes (Hocking 1991, 2000). Sediments of FA2 consist of mainly fine- to medium-grained thin-bedded sandstones, and are much more variable in their style of deposition. The difference in interpretation of the depositional setting of FA2 is important in understanding the significance of the trace-fossil fauna in models of early colonisation of the continental environment during the early Paleozoic. Arguments in support of the first interpretation are presented below.

Trewin (1993a, b) and Trewin & McNamara (1995) considered that the transition from FA1 to FA2 represented an overall reduction in fluvial processes and an increase in eolian processes in the younger sediments. Such a change in depositional style could reflect a reduction in rainfall resulting in increasing aridity and thus a reduction in sediment supply (Trewin 1993a). Trewin further suggested an alternative scenario, a shift in the area of fluvial deposition.

The second cycle of FA3 to FA4 is marked by the sudden reappearance of coarser, fluvial sandstones, suggesting a rejuvenation of the source area (Hocking 1991). Lithologically the sediments are very similar to those deposited in FA1, though FA3 differs from FA1 in having clear metre-scale fining-upward cyclicity. The transition from FA2 to FA3 could have arisen from an increase in paleoslope, resulting in an increase in depositional energy and thus grainsize (Trewin 1993a). Alternatively it may reflect increases in rainfall in the source area of the sediments to the southeast. Hocking (1991) considered that depositional energy levels were higher for the deposition of FA3, compared with FA1.

Sediments of FA3 are replaced higher in the section by sediments of FA4. These are a series of fining-upward cycles 0.5–2 m thick, from medium-grained sandstones to much finer siltstones. FA4 probably represents a higher energy fluvial-marine transition, although further research is required to validate this hypothesis.

Sediments of FA2

EOLIAN SANDSHEETS AND DUNES

FA2 is composed primarily of subparallel, bedded sandsheets up to 2 m thick, with internal laminae 1–5 cm thick, with low-angle cross-bedding typical of deposition in an eolian setting. The sandsheets are bounded on their upper surfaces by low-angle truncation surfaces and have inverse-graded millimetre-scale laminae characteristic of eolian ripples (Trewin 1993a). Bedding planes show adhesion ripples and eolian deflation ridges. Beds lacking the fine lamination often show wave ripples, typical of structures formed in shallow water. Many display evidence of subsequent exposure.

The low-angle (generally <20°) cross-bedding occurs in beds up to 2 m thick of well-sorted, fine- to medium-grained sandstones. The bases of the cross-bedded units grade into sandsheets which commonly show wind-ripple lamination (Trewin 1993a). From analysing patterns of cross-bedding Trewin (1993a) was able to demonstrate the straight-crested architecture of the dunes, many of which were at least 100 m wide. The upper surfaces of cross-bedded units locally show corrugations produced by

eolian scour. Moreover, foresets may be covered by low-amplitude eolian ripples. As Trewin (1993a) has pointed out, slip-face orientations of the cross-bedding consistently are directed to the southeast, rather than the northwesterly trends seen in the fluvial trough cross-bedding. This supports the notion that these were eolian dunes facing obliquely up the paleoslope. Between the dunes active deflation is thought to have occurred, resulting in the subsequent development of interdune pools. The absence of current ripples in these bodies of water led Trewin (1993a, b) to argue that flooding was not due to fluvial activity, but was generated by a more passive rising watertable following drier phases of eolian sand movement. Some shallow interdune pools show evidence of microbial mat development.

Much of the argument for the early establishment of a terrestrial freshwater ecosystem hinges on trace-fossil evidence from FA2. The rich trace-fossil assemblage in FA2 is characterised by an extensive suite of arthropod trackways (see below). The manner of their preservation lends support for the view that there was extensive eolian activity during the deposition of this facies. The trackways occur mainly in the sandsheet facies, as well as on sloping surfaces of small dune features. They are often on flat-topped rippled surfaces. Preservation of the trackways is very variable, from poorly defined clusters of footfalls that have merged into a single depression, to very commonly exquisitely preserved detail of each individual footfall, with small, discrete mounds of sediment piled up behind the imprint (Figure 4), or in the case of what is interpreted as a set of vertebrate footprints, finely preserved sand splashes produced by a more rapid flicking of the sediment during the locomotion stroke (see below).

The walls of the footprints are often steep-sided to vertical, the sand being sufficiently cohesive to the moment the foot was withdrawn from the sediment to retain the exact shape made by the footfall. Such preservation can only occur with such frequency on wet sand surfaces that are subaerially exposed (Hocking 1991 p. 33). Surface tension between sand grains will provide a rigid cohesive force over a wide range of degrees of water saturation (Scheel *et al.* 2008). Only in the extremely wet or extremely dry sands will the footprints be ill-defined. This wide range in water saturation levels that result in binding of sediment grains by surface tension is part of the reason for the preservation of so many trackways throughout FA2.

The other reason is that exposure by natural weathering of the tracks occurs at boundaries between abruptly changing grainsizes, almost invariably the footprint-imprinted sands being overlain by appreciably finer, very well-sorted sands. Such sands are here interpreted as having been deposited by eolian agencies. The deposition of the very fine sand is likely to have occurred as the wind velocity decreased, passively covering and protecting the finest details of the footprints. Hocking's (1991) scenario of deposition in a tidal flat is not supported by the style of footprint preservation. Any trackways made on an exposed tidal sand flat are likely to have been destroyed by the incoming tide. Although it could be argued that mud drapes during periods of still water could conceivably preserve such tracks, there is no sedimentological



Figure 4 Diplichnites trackway showing steep-sided footprints arranged in groups of three, with the inner pair getting out of phase with the outer pair because of their shorter length, causing them to have a greater stride distance. Note also the small mounds of sand pushed up by the appendages, confirming movement direction being from bottom to top. WAM 84.1634. From top of the gorge at The Loop; FA2. Scale bar 100 mm. Specimen on display in Diamonds to Dinosaurs Gallery, WA Museum, Perth. Photo by K Brimmell.

evidence in the Tumblagooda Sandstone for such events. Moreover, the lack of herring-bone cross-stratification in the sediments further argues against a tidal influence.

FLUVIAL SANDS

Interbedded with the sandsheets are moderately sorted medium- to coarse-grained sandstones, generally up to 3 m thick, but up to 8 m in some instances, with occasional mud clasts and small pebbles. These have been interpreted (Hocking 1991; Trewin 1993a, b) as having been deposited in fluvial channels and sheets. These units probably represent a sequence of flooding events, single events being represented by thinner cross-bedded units up to 50 cm thick. The thicker units are the equivalents of FA1 and locally show soft-sediment deformation (Hocking 1991). Trough cross-bedding is commonly seen in these thicker units, and erosional features occur at their bases. There is little evidence of the establishment of incised channels, deposition being mainly braided. Upper surfaces sometime show evidence of burrowing activity, suggesting periods of stability before the next flooding event.

Hocking (1981, 1991) traced thicker units for up to 3 km in a downcurrent direction. Architecture of the flows was sheet-like, diminishing in thickness downstream. In FA1 and FA3 current direction was generally northwesterly (Hocking 1991). In FA2 fluvial beds northwesterly paleocurrents are present in the coarser facies, but the interspersed sandsheets and dunes do not show the same northwesterly direction of flow. Rather, fluvial flow was to the southwest. Trewin (1993b) explained this difference as being due to water flow having been constrained by the orientation of the dunes (which ran southwest to northeast), resulting in flow parallel to the dunes and hence to the southwest. Why flow was not to the northeast is not clear.

The fluvial beds are likely to have been deposited on a large sandy outwash area by sheet runoff (Hocking 1991). The trough cross-bedded units demonstrate that despite being relatively thin, the beds had great lateral extent; channel features were rarely developed; current direction was strongly unimodal; and top bounding surfaces were planar. Trewin (1993a) argued that such features point to variable stream discharge in an environment lacking any resistant sediment-binding agent, such as plants, mud or early cement. Deposition at a time before any appreciable covering by land plants in the absence of vascular plants minimised channel stabilisation by plant roots (Davies & Gibling 2010). Deposition was almost entirely of medium- to coarsegrained sands, with little mud or silt being retained. This suggests that energy levels during stream flow were sufficiently high to transport finer grained sediments more distally into the marine environment.

Trewin (1993a p. 397) argued that it was likely that 'the water table exerted a strong influence on deposition of the aeolian sandsheet facies in that it would have provided a downward limit to deflation processes'. Due to the permeability of the Tumblagooda sands, the watertable is likely to have risen appreciably during periods of high discharge, resulting in deflation hollows and interdune areas flooding and producing short-lived pools of water in which some small arthropods were able to feed and flourish. Where they resided after the pools

dried out is not clear. Either they were sufficiently mobile to move to other pools, or were able to aestivate in the sand or perhaps, like some modern-day notostracan crustaceans, laid eggs which hatched out when the pools were reactivated.

TUMBLAGOODA SANDSTONE ECOSYSTEM: ICHNOFABRICS AND THEIR IMPLICATION FOR FRESHWATER DEPOSITION

In their description of the trace-fossil fauna of the Tumblagooda Sandstone, Trewin & McNamara (1995) identified 27 different types of trace fossils. The traces were assigned to two ichnofaunas: the Heimdallia-Diplichuites Ichnofauna, present in FA2, and the Skolithos-Diplocraterion Ichnofauna, present in FA3 and FA4 (Trewin & McNamara 1995 figure 6). Trace fossils are absent in FA1. The various trace fossils that have been described can be categorised based on the behaviour of the animals that made them. These are: (i) locomotory tracks thought to have all been made, with one exception, by arthropods; (ii) locomotory trails; (iii) resting traces; (iv) dwelling traces; (v) hunting (predation) traces; and (vi) feeding traces. This range of activities, particularly in the trace-fossil fauna present in the mixed fluviallacustrine-eolian FA2, provides support for the idea that this association of trace fossils comprises evidence of the establishment of a relatively complex freshwater terrestrial ecosystem in this part of the Tumblagooda Sandstone during the Early to mid-Silurian.

In this review I assign those traces that form the Heimdallia-Diplichnites Ichnofauna to the Scoyenia ichnofacies. This ichnofacies is confined to FA2. Buatois & Mángano (2004) pointed out how the ichnofacies model originally proposed by Seilacher (1963, 1967) (called by him 'facies' rather than 'ichnofacies'), can be applied to trace-fossil assemblages formed in both continental and marine environments. Seilacher (1967 p. 415) proposed a single ichnofacies for all continental environments, which he called the 'Scoyenia facies' for 'non-marine sands and shales, often red beds, with a distinctive association of trace fossils'. This ichnofacies is characterised by the presence of arthropod trackways and bilobed traces and meniscate burrows. However, a number of authors have noted (Frey & Pemberton 1984, 1987) that this ichnofauna formed under rather distinct environmental conditions, typified by low-energy setting that oscillated between aquatic and non-aquatic, subaerial, conditions. Buatois & Mángano (2004) now recognise four continental ichnofacies, of which the Scovenia ichnofacies is but one. It is redefined (Frey et al. 1984; Buatois & Mángano 1995, 2004) as consisting of horizontal meniscate backfilled traces produced by mobile deposit feeders; locomotion traces, both trackways and trails; vertical dwelling burrows; a mixture of invertebrate (predominantly arthropod), vertebrate and plant traces; low to moderate ichnodiversity; and localised high abundance.

The Tumblagooda Sandstone ichnofauna fulfills all of these criteria, apart from the absence of plant material, on account of the pre-vascular plant age of the formation. As Buatois & Mángano (2011 p. 75) have pointed out, the

abundance of meniscate traces and arthropod tracks is 'typical of sediments periodically exposed to air or periodically inundated, and intermediate between aquatic and terrestrial environments'. As I will discuss, the preservation of many of the trace fossils in the Tumblagooda Sandstone is due to their primary formation as traces in a subaerial environment, but at the margin of quiet bodies of freshwater.

Compared with the Scoyenia ichnofacies, the Skolithos ichnofacies in FA4 is far more restricted in its diversity. It is characterised by the dominance of vertical, cylindrical burrows made by suspension feeders or passive predators; occurrence of spreite U-shaped equilibrium burrows; abundant three-dimensional burrows with a major vertical component; scarcity of horizontal traces; low diversity; and variable abundance (Buatois & Mángano 2011). Although the Skolithos-dominated tracefossil fauna of FA4 fits well in this diagnosis of the ichnofacies, it differs in one significant respect in that Buatois & Mángano (2011) have suggested that in fossil examples of the Skolithos ichnofacies horizontal traces are not preserved, due to the high energy of the depositional system. Although not described in Trewin & McNamara (1995), arthropod tracks have been found in the trace fossil assemblage in FA4, along with Aulichnites trails, as discussed below.

Scoyenia ichnofacies

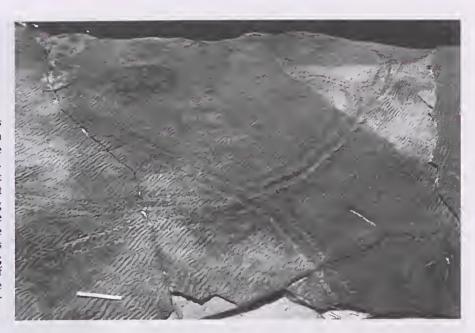
ARTHROPOD LOCOMOTORY TRACES

The most diverse horizontal locomotory traces in the Tumblagooda Sandstone are those made by arthropods, consisting of essentially parallel rows of pits often many metres in length. Arrangement of pits made by multiple footfalls varies between rows of discrete sets of repeated groupings of imprints (allowing assessment to be made of the number of walking legs) to less well-defined sets where leg number of the originator cannot be ascertained due to overprinting of footfalls. These arthropod trackways vary greatly in size from a minimum observed width of 5 mm between rows of appendage imprints (Figure 5), to the largest at about 300 mm. There is appreciable variation in trackways in the number of



Figure 5 Smallest known example of *Diplichnites*. Field specimen in the bottom of the gorge, western side of The Loop; FA2. Diameter of coin 19.4 mm.

Figure 6 Large Diplichnites trackways, about 18 cm in width crossing rippled marked sand at The Fourways, Murchison River; FA2. The pair coming in from the left seem to coalesce and the resultant single track becomes deeper, losing definition, perhaps due to one arthropod having climbed on the back of the other. This scenario is supported by the tracks becoming shallower following separation of the tracks. It is a matter of pure speculation as to the nature of their behaviour. Ruler 40 cm long.



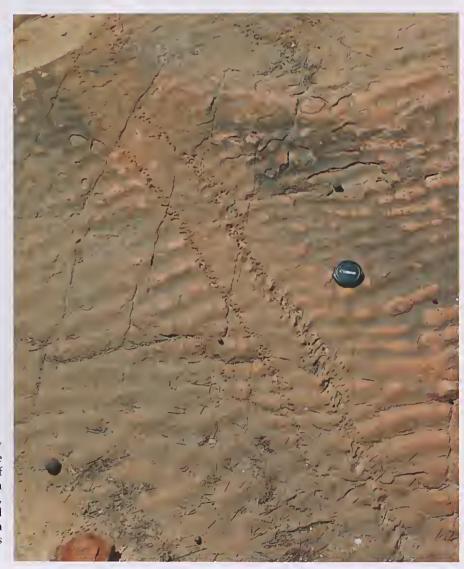


Figure 7 Diplichnites trackway crossing ripple marked surface showing repeated patterns of footfalls, suggesting formation by an arthropod, perhaps a euthycarinoid, with up to 11 pairs of legs. Field specimen at bottom of gorge on western side of The Loop; FA2. Lens cap diameter 55 mm.

imprints in each series, due to variations between taxa in the number of walking appendages; in spacing arising from variable speed of locomotion; and in degree of detail of the imprints, arising from differences in condition of the sediment at the time of formation of the imprints, in particular the degree of water saturation of the sediment. Those trackways made subaerially in sands that were either very dry or very wet are usually illdefined, and series of imprints often merge together to form single, elongate grooves. However, trackways made in sands with a relatively wide degree of water saturation that provides sufficient surface tension to hold sand grains in contact, but not enough water to fill the pore space entirely, as this would cause collapse of the sand, can often show extremely good detail (Scheel et al. 2008). Thus not only can the numbers of appendages used in walking sometimes be calculated, but so too can the direction of stroke and the sequence of appendage usage.

Trackways can also show evidence of a single, broad central drag mark, or a pair of thin drag marks, produced by a ventral appendage or the tail. Forms without a central drag mark are the most common and are assigned to the ichnogenus *Diplichnites* (Figures 2, 4–10); those with a deep, single groove, and widely spaced groups of appendage imprints to *?Paleohelcura* (Figure 11); those with a broad central drag mark to *Protichnites* (Figures 12, 13); while those with a pair of thin, parallel grooves were assigned to *Siskenia* (Figures 14, 15) by Trewin & McNamara (1995). Lengths of trackways vary from a few centimetres up to 10 m, the most spectacular being near Fourways where five well-defined tracks, each several metres in length, were formed on a wet, rippled surface (Figure 6).

A very wide variety of forms can be assigned to *Diplichnites*. In addition to morphological differences arising from a wide taxonomic diversity of arthropod track makers, this is also due to variability in behaviours of the track makers. This may, in part, be influenced by the consistency of the sediment across which they were walking and the consequent preservational effects in sands of variable water saturation levels. Trewin & McNamara (1995) somewhat arbitrarily subdivided the *Diplichnites* trackways into three groups, types A, B and C, based on track width and form of the imprints. These are likely to have been made by a variety of different arthropod taxa, morphological differences indicating perhaps by as many as 10 different types.

Diplichuites type A consists of small trackways, generally between 5 and 40 mm in width (Trewin & McNamara 1995 figure 19a). They are usually straight to gently curved, simple with a single row of evenly spaced conical to elongate imprints, which sometimes may be connected by a shallow groove. These tracks are in phase and the track rows are spaced at intervals a little less than half the external trackway width. Where the tracks curve they reveal a series of generally about five imprints at a very low angle to the midline. These tracks may have been made by a xiphosuran (Trewin & McNamara 1995).

Diplichmites type B trackways are the most common and are usually between 50 and 200 mm in width. They possess elongate imprints arranged at a high angle to the direction of travel. Often the imprints are superimposed. Two interpretations have been proposed as to how to

calculate the number of walking appendages possessed by the originator of the trackway. One suggests up to 11, the other interprets them as being in groups of three. Uncertainty arises from the fact that one of the group of three imprints gets out of phase with the other two (Figure 4). As a consequence, the out of phase imprints gets progressively closer to the midline before moving laterally as it gets back into phase with the other pair of imprints on a gentle sinusoidal curve. This could occur if this more anterior of the group of three appendages was appreciably shorter than the other two, which would be of similar length to each other.

In other types of trackways where oblique sets of up to 11 imprints occur, and where the two sets on either side of the trackway parallel one another, but are slightly offset to the main direction of the trackway (Figure 7), the originator of such tracks probably possessed up to 11 pairs of walking appendages (Figure 8). Given that the only body fossil found in the Tumblagooda Sandstone, *Kalbarria*, is a euthycarcinoid with 11 pairs of walking legs (Figure 2), it is not unreasonable to suggest that it could have been responsible for making many of these trackways. In those examples where sets of slightly



Figure 8 Diplichnites trackway showing repeated patterns of footfalls, suggesting formation by an arthropod, perhaps a euthycarinoid, with up to 11 pairs of legs. From top of the gorge eastern side of The Loop; FA2. Specimen on display in Diamonds to Dinosaurs Gallery, WA Museum, Perth. Scale bar 100 mm.

oblique groupings of 10–11 imprints are not parallel to each other and are both directed toward the midline, this is probably due to the offsets caused by the smaller appendage length of the anterior pair, the originator having just three pairs of walking appendages. As discussed below, there is evidence in some trackways of the originator having possessed at least one paddle-like pair of appendages. This, combined with locomotion on three pairs of appendages, suggests creation by a eurypterid.

Diplichmites type C trackways are the largest, generally between 200 and 300 mm in width (Figure 9). They are characterised by the possession of elongate, slit-like imprints directed at about 45° to the midline. The individual imprints may be up to 40 mm long and 15 mm wide. Two to three imprints occur in each group, but again they may get out of phase. As with other examples of *Diplichuites*, the imprints are in phase.

While the *Dipliclinites* forms A–C generally have either imprints formed as conical pits, or as elongate slits, depending on the speed of locomotion of the originator, some forms attributable to *Dipliclinites* have more complex imprints. Conical pits and slits would have been made by narrow arthropod walking legs that probably terminated in a relatively sharp point. However, trackways such as WAM 84.1647 have impressions made by much broader, paddle-shaped appendages. Specimen



Figure 9 Large *Diplichnites* trackway about 25 cm in width. Field specimen, bottom of the gorge, eastern side of The Loop; FA2. Diameter of coin 28.5 mm.



Figure 10 Unusual *Diplictmites* trackway formed by an arthropod sinking into the sediment producing a drag mark made by the right hand side of its body. Limbs on the left side were probably held out almost horizontally as the animal tried to get purchase. On the right side imprints of paddles and semicircular grooves made by paddles suggest that the track might have been made by a eurypterid. WAM 84.1647 from near The Loop; FA2. Scale bar 30 mm.

WAM 84.1647 was made by an animal that may have been walking along the edge of sloping surface, causing the right hand side of its body to drag on the sand. Impression of the paddle-spaced appendage and of the sweeps it made as it propelled itself through the sediment are preserved (Figure 10). These are very reminiscent of eurypterid paddles (appendage VI).

Much less common than Diplichnites are arthropod trackways that also have a central drag mark, made either by a distal posterior terminal piece, or by a ventral sagittal appendage, such as a genital appendage (Braddy & Dunlop 1997). Although uncommon, such trackways show high diversity, varying in imprint architecture, and form and nature of the central drag mark. The largest is known from a series of overlapping trackways (WAM 84,1657) that were assigned to ?Paleohelcura antarcticum by Trewin & McNamara (1995). The trackways are rather disordered and, on the basis of the number of drag marks, represent four individuals (Figure 11). The most complete is about 160 mm in width, with individual footprints making large (up to 20 mm diameter) conical depressions that are up to 40 mm deep (Trewin & McNamara 1995). The central drag mark is up to 20 mm in width and in one instance shows a termination with a plug of sand at the end, suggesting that the structure that made the drag mark was able to be lifted from the surface of the sand during locomotion.



Figure 11 *?Paleohelcura* trackways with well-developed median grooves. WAM 84.1657, from top of the gorge near The Loop; FA2. Scale bar 100 mm. Photo by K Brimmell.

Trewin & McNamara (1995) suggested that these tracks could have been made by a scorpionid. However, the lack of a genital appendage in Paleozoic forms, such as *Gigantoscorpio*, argues against this interpretation. The similarity to an arthropod trackway from the Silurian of Ringerike, Norway described by Hanken & Størmer (1975) attributed to the eurypterid *Mixopterus*, suggest that the Tumblagooda trackway may also have been made by a eurypterid.

A distinctive, but very different, trackway from both *Diplichnites* and *?Paleohelcura* is a relatively uncommon form attributed to *?Protichnites* by Trewin & McNamara (1995). Examples are known that are about 75 mm in width. They are characterised by a series of closely spaced footprints that lie close to the midline, down which runs a broad drag mark. Each set of footprints consists of a group of ill-defined multiple footfalls that landed in roughly the same space, causing poor definition. These square to rectangular imprints are both closely and regularly spaced, about 25 mm apart, as well as being closely aligned to the broad, smooth drag mark which is up to 20 mm in width and is flat, apart from a

narrow, raised rim formed from the sediment having been laterally displaced during locomotion (Figure 12). It is not clear what organism was responsible for making this type of trackway. Despite the arguments of Collette *et al.* (2012), it is very unlikely to have been made by a euthycarcinoid.

In describing a series of trackways from the Cambrian Elk Mound Group of Wisconsin, which they assigned to Protichnites, Collette et al. (2012) inferred that trackways described by Trewin & McNamara (1995) from the Tumblagooda Sandstone support the assertion that the Elk Mound trackways were made by euthycarcinoids. This is not so. While ?Protichnites from the Tumblagooda Sandstone and Protichnites from the Elk Mound Group appear to be congeneric, no evidence or argument was presented by Trewin & McNamara (1995) to suggest that trackways with a central groove were made by euthycarcinoids. This group of arthropods is represented in the Tumblagooda Sandstone by Kalbarria brimmellae (McNamara & Trewin 1993) (Figure 2). From the same horizon as the body fossil, there are abundant trackways. and all are Diplichnites. In other words they lack a central drag mark. Moreover, where it is possible to ascertain the number of repeated sets of appendage imprints, these show the possession by the track originator of 11 pairs of appendages. This is the number of legs possessed by Kalbarria.



Figure 12 ?Protichnites trackway showing closely spaced footfalls and broad median groove. Trackway crossing surface with Heimdallia burrows. WAM 97.952; FA2. Scale bar 50 mm.



Figure 13 Unnamed trackway probably made by the arthropod responsible for the ?Protichnites trackways walking through poorly consolidated rippled sands. Field specimen, top of the gorge at The Loop, north of Nature's Window; FA2. Pen 12 cm long.

One field example is known of an unnamed trackway that represents the *?Protichnites* animal walking through very wet, rippled sand. Due to the high water-saturation levels there is no detail of individual footfalls, merely a pair of grooves representing where the animal ploughed through the sloppy sediment. The central drag mark forms a similar depth to the lateral drag marks made by the appendages (Figure 13).

Another uncommon arthropod trackway with a drag mark between the imprints of the footfalls is Siskemia. This generally small trackway, reaches up to about 90 mm wide and is typified by the possession of a pair of very narrow grooves. These can be up to about 15 mm apart. Sometimes they run down the midline (Figure 16), but in some examples they drift from side to side (Figure 14) or are close to one set of imprints (Figure 15). This suggests that the structure that made the drag marks was not fixed rigidly to the ventral surface of the arthropod body, but was articulated, allowing for a certain degree of lateral movement. Interestingly, in their discussion of the morphology of the genital appendage of the eurypterid Baltoeurypterus tetragonophthalmus, Braddy & Dunlop (1997) described the sexual dimorphism in this structure, highlighting that the form that may be the male possesses an appendage which terminally ends in a pair of strongly acuminate structures. If such an appendage were dragged along a sediment surface it would produce a trail very reminiscent of the central drag mark in Siskemia.

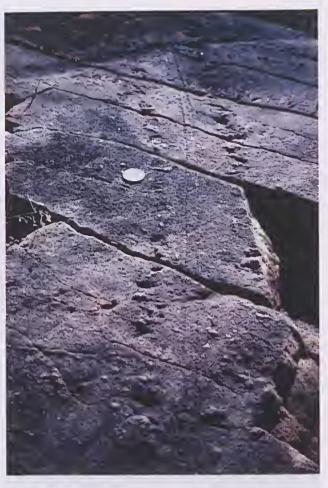


Figure 14 Siskemia trackway showing distinctive thin double grooves between footfalls. Field specimen near Z Bend; FA2. Diameter of coin 28.5 mm.

One example of Siskemia is known (Figure 15) that shows the faint double drag mark typical of the ichnogenus, and repeated patterns of nine footfalls. Moreover, this trackway was made by the arthropod walking along a strandline at the edge of a body of water. To one side are well-developed adhesion ripples, formed by the wind blowing over very wet sand, alongside a flatter, slightly drier sand surface upon which the Siskemia trackway was formed. Some Diplichnites trackways also show evidence of such a foraging strategy. A number of examples have been found where Diplichnites trackways similarly run parallel to paleostrand lines that flanked desiccating bodies of water. Such perambulations may reflect arthropods foraging along the margins of pools of water, and feeding upon stranded organic matter.

TETRAPOD LOCOMOTORY TRACE

One trackway (cast - WAM 12.12.1) in the FA2 facies is completely different from all other trackways ascribed to formation by arthropods. It is 18 cm wide and extends for 45 cm. Seven equally spaced imprints can be identified on its right side, and six on its the left. Individual foot impressions are rhombic in shape and very large, being 3.5–5 cm wide and 3 cm long, and set between 4 and 6 cm apart (Figure 16). The imprints are



Figure 15 Siskemia trackway with paired grooves closer to one set of footfalls. Individual walking along edge of body of water. To its left adhesion ripples formed by wind blowing over very wet sand surface. Field specimen from near The Loop; FA2, Scale bar 100 mm.

far larger than those made by individual arthropod footprints and completely different in shape. Even merged clusters of arthropod imprints which often develop when they have walked through very wet sand, are not as large as these and do not form the same shape. The rhomboidal form is unique among Tumblagooda Sandstone imprints. The fine details preserved in some of the impressions shows that they have not been formed by the coalescence of clusters of fine arthropod imprints. Opposite impressions are offset by about half an impression length. Four of the impressions show exquisite detail of what are interpreted as multi-digit imprints (Figure 17). The direction of limb movement during locomotion is shown by the orientation of the grooves left by the larger, adaxial digits, and by the orientation of the slightly sinuous, narrow ridges of sand that were formed as the sand was thrown sideways and backwards by the animal as it moved forward. The adaxial two digits were evidently the largest (both longer and broader than the others), and like the other digits they pointed anteriorly (Figure 17). The impressions made by these two larger digits are flanked by elongate grooves, seemingly made by four digit-like structures of similar size. These in turned are flanked by a pair of much smaller elongate impressions, indicating that the foot possessed a total of eight digit-like structures.

The 'sand splashes' created by the movement of the feet indicate that the trackway was made subaerially (Figures 16, 17). Such structures have never been observed in any arthropod trackways in the Tumblagooda Sandstone. Instead, arthropod footfalls only produced small mounds by the action of the fine, narrow appendages entering the sand at a high angle (Figure 4). Many of the impressions from specimen WAM 12.12.1 show evidence of multiple sand splashes from each propulsive event (Figure 17). Moreover, there is a direct correlation between each sand splash ridge

Figure 16 Plaster cast of mould of two sets of trackways (WAM 12.12.1). Running from left to right is a Siskemia track. Running across this is a trackway made by an animal with broad, digitate feet, interpreted as a tetrapod. Sand splashes present in bottom left corner of footprints on left hand side, and bottom right on right hand set of imprints attest to formation subaerially. These also show details of individual forwardly facing digits, which are broader closer to the midline. Based on field specimen downstream from The Loop; FA2. Scale bar 50 mm.





Figure 17 Close up of individual imprints on right hand side of trackway interpreted as having been made by a tetrapod. Photograph of field specimen, clearly showing imprints of digits and sand splashes caused by movement of the feet during locomotion. Field specimen downstream from The Loop; FA2, Scale bar 70 mm.

and the 'digit'. Whereas some sand splash ridge are straight, others are sinusoidal. This suggests independent movement of the digits.

Development of sand splash ridges implies reasonably rapid movement of the appendage during propulsion, with the wet sand being flicked out during the propulsive stroke. It is possible to suggest how the manus/pes rotated during propulsion from the orientation of the digit grooves and the corresponding sand splash ridges. The grooves extend almost exsagittally, but the sand splash ridges are orientated posterolaterally, indicating an initial posterior movement of the digits while in contact with the substrate, followed by a lateral rotation as the manus/pes was lifted from the substrate during the last part of its backstroke. The rotation of the manus/pes is responsible for the deeper excavation of the impression adaxially.

It is difficult not to come to the conclusion that the animal that made this track was tetrapodous and digitate. Such an interpretation clearly raises some major issues for our understanding of the sequence and timing of the origin of tetrapods and their activity on land. Currently the oldest described evidence for tetrapods are

trackways from the Middle Devonian of Poland (Niedźwiedzki et al. 2010). The imprints of the manus and pes of these trackways are very similar in appearance to the tetrapodous Tumblagooda trackway. Stride pattern is also comparable in the two forms. With the earliest skeletal evidence of tetrapods being the Late Devonian Acanthostega and Ichthyostega from east Greenland (Long & Gordon 2004), and the earliest undoubted terrestrial skeletal tetrapods not being know until the early Carboniferous, suggesting that terrestrial tetrapods existed in the early to mid-Silurian might seem foolhardy. But hopefully further material will be forthcoming from the Tumblagooda Sandstone to support the evidence provided by WAM 12.12.1, along with more empirical data concerning the age of the unit, to argue unequivocally that tetrapods were present in the Silurian and were part of the colonisation of land by animals. It could, of course, be argued that the tetrapodous condition in vertebrates may have originated more than once, the first time in Gondwana.

RESTING TRACES

In addition to locomotory behaviour, arthropod activity in the Tumblagooda Sandstone also includes evidence of scratch marks made by multilimbed arthropods, arising from either locomotion partially through the sediment, or from feeding activity. Resting traces that show evidence of the ventral elements of the arthropod are also relatively common. These often show an effective outline of the underside of the arthropod, particularly the scratch marks made by individual appendages (Figures 18, 19). There has been a tendency in the literature to ascribe the formation of *Cruziana* and *Rusophycus* to trilobites (Seilacher 1985; Buatois & Mángano 2011), but the presence of these trackways in a freshwater/eolian subaerial setting clearly shows that they can be made by other types of arthropods. One large *Cruziana* (WAM



Figure 18 Resting trace *Rusophycus*, possibly made by a euthycarcinoid. Pair probably made by same individual. Field specimen at bottom of the gorge, western side of The Loop; FA2. Lens cap diameter 55 mm.



Figure 19 Hunting trace *Seleniclinites* (crescentic form on left) and resting trace *Rusophycus* (to its right), probably made by the same individual euthycarcinoid, possibly hunting for small organisms that occupy 1–2 mm diameter *Diplocraterion* burrows on same surface. Top of ridge, 500 km north of Nature's Window, The Loop; FA2. Pen 12 cm long.

92.635) has been found in the Tumblagooda Sandstone (Trewin & McNamara 1995). It shows a broad, double series of scratch marks angled at about 55° to the midline made by an arthropod with uniramous legs, as only one set of scratches is evident. Given the size (a width close to 80 mm), this was probably made by the same type of arthropod that made some of the larger *Diplichnites* trackways.

Examples of Rusophycus are more common. Rusophycus trefolia Trewin & McNamara 1995, was described from the Tumblagooda Sandstone on the basis of numerous relatively small, oval traces with paired scratch marks, or impressions of the appendages (Figure 18). These vary in width from 20 to 60 mm. Many are deeper at one end, which probably represents where the animal initially partially burrowed into the sand. Many show a trefoil shaped structure at one end, that may reflect the shape of the anterior feeding appendages (Figure 18). The scratch marks in these traces are more widely spaced than those that occur in Rusophycus made by trilobites, probably reflecting the uniramous nature of the originator, rather than the bilobed appendages of trilobites. The most likely candidate for the production of these small Rusophycus in the Tumblagooda Sandstone are euthycarcinoids, on account of comparable size and possession of multilimbed uniramous appendages.

DWELLING TRACES

Evidence that the environment in which the Tumblagooda Sandstone was deposited was, at times, conducive to the establishment of a permanent or semipermanent freshwater ecosystem is shown not so much by the activity of arthropods walking across the surface of exposed sand flats, but by the establishment of dwelling traces and feeding burrows. The most common dwelling trace in the *Scoyenia* ichnofacies in FA 2 is *Diplocraterion*. Here it consists of very small U-shaped vertical burrows, with each burrow being only 1–2 mm in diameter (Figure 19), and set between 10 and 35 mm apart (Trewin & McNamara 1995 figure 22). The burrows are rarely more than 35 mm deep, and spreite are developed in the zone between the burrows (Schlirf 2011). *Diplocraterion* often occurs with *Rusophycus* and *Selenichnus* (see below) on the tops of fluvial channels.

Larger vertical burrows are represented by *Tigillites* (Trewin & McNamara 1995 figure 38), a much more irregular burrow system, with individual burrows about 10 mm in diameter, arranged in irregular rows up to 140 mm long. It has been suggested that these may represent failed attempts to establish more permanent feeding burrows by the organism that constructed *Heimdallia* (Trewin & McNamara 1995), as discussed below.

The largest burrows are horizontal to partially inclined meniscate burrows up to 150 mm wide and up to 500 mm in length that have been assigned to *Beaconites*. The burrows are straight to gently curved and infilled with backfilled packets of sediment (Figure 20). Morrissey & Braddy (2004) have suggested that *Beaconites* in the Lower Old Red Sandstone in south Wales could have been made by an eoarthropleurid myriapod. Fayers *et al.* (2010) have suggested that the enigmatic arthropod



Figure 20 Dwelling burrow *Beaconites*. Field specimen at bottom of gorge, western side of The Loop; FA2. Lens cap diameter 55 mm.

Bennettarthra from the same Lower Devonian horizon could also have been responsible for the formation of the Beaconites and Diplichnites that occurs in association. It is probable that some of the organisms responsible for production of some of the smaller Diplichnites trackways in the Tumblagooda Sandstone were similarly responsible for the formation of the Beaconites burrows.

FEEDING TRACES

The most extensive vertical burrows have been assigned to *Heimdallia* (Figures 21–23). This is a complex burrow



Figure 21 Feeding trace *Heimdallia* showing well-developed spreite structures. WAM 84.1765a; FA2. Scale bar 50 mm.

form with both a vertical and horizontal component. It occurs in the sandsheet facies, sometimes in waverippled units or in microbial mats. In plan view the burrows are straight to extremely sinuous, with a width of 5–20 nm. The burrows are vertical to steeply inclined and generally about 120 mm deep, with backfill units about 5 mm thick. These reduce in inclination with depth (Trewin & McNamara 1995). *Heimdallia* can occur in large numbers, resulting in extensive bioturbation of beds many square metres in area. Individual beds are in the order of 120 mm thick, but these can occur in repeated units over 1 m thick (Trewin & McNamara 1995).

Bradshaw (1981), in describing similar Heimdallia burrows from the Devonian of Antarctica, considered that they were made by arthropods mining the sand, and extracting organic material. The extent of Heimdallia-rich beds in the Tumblagooda Sandstone implies that periodically the shallow-water bodies in which they formed were organically very rich, possible in algae or bacteria, or both. As Trewin & McNamara (1995) have suggested, this may explain why the sediment would have been sufficiently cohesive to preserve the burrows. In his study of Lower Carboniferous examples of Heimdallia from Ireland, Buckman (1996 p. 50) interpreted them as feeding structures 'formed from a horizontal basal tube by repeated cycles of probing and withdrawal in an upward vertical vector, with forwards movement occurring at the end of each cycle... resulting in the production of a 'spreite' structure.'

Another, much less common, burrow is *Didymaulyponomos*. This occurs as narrow, horizontal burrows up to 10 mm wide, but up to 700 mm in length (Trewin & McNamara 1995 figure 16), often in dense accumulations. The burrow infill structure sometimes shows a beaded structure.

HUNTING (PREDATION) TRACES

Heimdallia beds are often associated with the much larger horizontal burrow *Tumblagoodichnus* (Figures 23, 24). These are large burrows, generally 45–80 mm wide and horizontal to subhorizontal, and up to about 400 mm long, though most would be little more than half this



Figure 22 Bedding surface with feeding trace *Heimdallia* and microbial mats. Bottom of gorge western side of The Loop; FA2. Lens cap diameter 55 mm.



Figure 23 Bedding surface with extensive feeding trace *Heimdallia* and palimpsest ripples and the hunting burrow *Tumblagoodichuus*. Bottom of gorge western side of The Loop; FA2. Lens cap diameter 55 mm.

length. Where suitably preserved, the burrow shows a wide, convex median ridge. Trewin & McNamara (1995) suggested that the trace was made by an arthropod making 'scoops' into a wet sand surface, pushing the sand aside or upwards. Examples are known (Figure 24) where the sand has been pushed anteriorly and forms a crescentic mound at the front of the burrow, providing evidence for the direction of movement of the burrow creator. *Tumblagoodichnus* burrows in *Heindallia*-rich beds could represent hunting traces made by the arthropod, feeding on the organism responsible for making the *Heindallia* burrows.

Another trace fossil, Didymaulichnus, resembles Tumblagoodichnus in consisting of relatively short and narrow horizontal grooves with a central raised ridge (Trewin & McNamara figure 15). However, Didymaulichnus is an order of magnitude smaller than Tumblagoodichnus. It is less than 10 mm wide and rarely longer than about 50 mm. It inevitably occurs in clusters, so possibly represents grooves made by the same animal digging at a very shallow angle into the sediment.

Another association that further illustrates the well-developed trophic structures within this nascent freshwater ecosystem and which can possibly be interpreted as a predator–prey relationship, is the frequent co-occurrence of *Diplocraterion* with *Rusophycus* and *Selenichuites* (Figure 19). This latter ichnogenus is a crescentic hollow, deeper at one end than the other. Most are 40–60 mm in width, reaching maximum anterior depths of up to 20 mm. The anterior margin may be

inclined to vertical, or even overhanging in some instances (Trewin & McNamara 1995). The posterior end has a raised trefoil-shaped structure, which also occurs in *Rusophycus*. The lateral margins of *Selenichuites* may, like *Rusophycus*, sometimes show transverse scratch marks. *Sclenichuites* can occur in very large numbers, with scores on the same bedding surface and often aligned in linear groups (Figure 25). These are likely to represent the activity of a single animal, repeatedly digging in the sand at low to high angles hunting for the *Diplocraterion* animal (Trewin & McNamara 1995 figure 33).

If Rusophycus represents the animal lying horizontally on a wet sand surface, then Selenichnites is the product of the arthropods' feeding behaviour. The occurrence of these dense clusters of Selenichnites and Rusophycus in sandsheet facies which are riddled with Diplocraterion suggest that the animal that made these U-shaped burrows was the target prey for the Selenichnites/Rusophycus animal. As discussed above, the likelihood that Rusophycus was made by a euthycarcinoid, such as Kalbarria, implies that it was also responsible for Selenichnites.

Skolithos ichnofacies

LOCOMOTORY TRACES

These are rare in the *Skolithos* ichnofacies. A single well-developed *Diplichuitcs* trackway occurs south of Red Bluff, and is preserved in a thin-bedded, fine sandstone



Figure 24 Hunting burrow *Tumblagoodichnus* in bioturbated bed of *Heindallia* showing mound of sand pushed up by animal is it ploughed horizontally across the surface of the sand, presumably hunting for its prey; from surface in Figure 23. Lens cap diameter 55 mm.

reminiscent of the sand sheet facies of FA2. Even in the generally appreciably coarser sands of FA4 short segments of *Diplichnites* occur. The other locomotory trace *Aulichnites*, has not been found in the *Scoyenia* ichnofacies. It consist of sinuous, gently convex-upward trails, up to about 15 mm wide, with a weak longitudinal furrow (Figure 26). The traces can cover surfaces of many square metres. Although generally regarded as having been made by gastropods, Trewin & McNamara (1995) point out that arguments have been made for a xiphosurid origin (Chisholm 1985).

DWELLING TRACES

The most extensive dwelling traces are Skolithos (Figure 27). In the Tumblagooda Sandstone they consist essentially of vertical infilled burrows generally 10-15 mm in diameter, but sometimes up to 25 mm (Trewin & McNamara 1995). They may extend for up to 1 m in length and are particularly common in the upper part of FA4 in the area around Red Bluff (Figure 23). The burrows show slightly greater cementation than the surrounding sands, resulting in them weathering out from the surrounding sediment, perhaps due to the higher organic content in the burrows during early cementation. Although many of the numerous occurrences of Skolithos in other early Paleozoic clastic sequences are in sediments interpreted as being of shallow, high-energy marine origin, Woolfe (1990) suggested they may also be found in eolian, fluvial or even lacustrine settings (Netto 2007). Therefore, using Skolithos as an indicator of marine sedimentation may not always be appropriate.

The U-shaped burrow *Diplocraterion* in the *Skolithos* ichnofacies is generally larger than in the *Scoyenia* ichnofacies, with individual burrows up to 15 mm in diameter, paired openings spaced up to 50 mm apart and up to 100 mm deep. As Trewin & McNamara (1995) have observed, the forms of *Diplocrateriou* in the Tumblagooda Sandstone are very similar to those that occur in the Early Devonian Old Red Sandstone in Scotland where



Figure 25 Hunting burrows Selenichuites, possibly made by just one or two individuals. Top of ridge, 500 km north of Nature's Window, The Loop; FA2. Pen is 12 cm long.



Figure 26 Locomotory trace *Aulichnites*. Car park 100 m north of Red Bluff; FA4.



Figure 27 Dwelling burrows Skolithos. Red Bluff. FA4.

they also occur with arthropod trackways in non-marine settings. Larger forms in the Tumblagooda Sandstone are closely associated with *Skolithos* burrows, such an association being typical of high-energy, mobile-sand settings.

Another dwelling burrow unique to FA4 is *Lunatubichnus* (Figure 28). These vertical burrows, up to 20 mm across and 70 mm deep have a crescentic cross-section, with a vertical groove often present in the convex inner wall. The crescentic cross-section is often, though not invariably, symmetrical. The burrows occur in clusters orientated in the same direction. Unlike *Skolithos*, these burrows are not infilled by sediment. The orientation of the burrows implies creation by a bilaterally symmetrical filter-feeding animal orientated into the direction of current flow (Trewin & McNamara 1995).



Figure 28 Dwelling trace *Lunatubichnus*. WAM 96.410a. Red Bluff, FA4. Scale bar 10 mm.

FEEDING TRACES

Evidence for possible feeding traces in the Skolithos ichnofacies is provided by the bell-shaped Daedalus (Trewin & McNamara 1995 figure 14). This trace consists of a vertical burrow shaft, the base of which flares out into a labyrinth of overlapping curving tubes, of similar width to the vertical shaft. The burrows are generally about 10 mm wide, with a vertical shaft up to 300 mm long and the basal bell-shaped convoluted burrows up to 120 mm across. Series of these burrows sometimes occur on single bedding planes, suggesting either a physical restriction to the depth of burrowing, or else attainment of an optimum feeding level. As Trewin & McNamara (1995) have pointed out, the similarity in form and size of the vertical shaft of Daedalus to Skolithos suggests the possibility that the two trace fossil types could have been constructed by the same type of animal.

Hocking (1991 figure 71) has illustrated a fine example of large burrows seen in cross-section, which might be attributable to either *Beaconites* or to *Tumblagoodichnus* in beds associated with *Skolithos*, suggestive of predatory activity by the larger horizontal burrow creator (R M Hocking pers. comm. 2013).

EARLY PALEOZOIC COLONISATION OF FRESHWATER AND TERRESTRIAL ENVIRONMENTS

The paleontological evidence for the colonisation of terrestrial and freshwater environments during the early Paleozoic comes not from body fossils but from studies of trace-fossil assemblages, such as those in the Tumblagooda Sandstone (Buatois & Mángano 1993, 2004, 2011; Buatois et al. 1998). By integrating trace fossil, sedimentological and paleobiological data dealing with the patterns of colonisation of the land by, predominantly, invertebrate biotas, the scope and extent of the first freshwater and terrestrial ecosystems can be established. Assemblages of trace fossils occur in a number of redbed early Paleozoic fluvial-lacustrineeolian sequences that range in age from Late Ordovician to Devonian. This period represents a critical phase in the evolution of life on Earth. Not only were invertebrates and vertebrates beginning to migrate from aquatic environments onto the much harsher terrestrial world, but the evolution of terrestrial plants was undergoing a profound revolution, as vascular plants evolved and expanded during this period.

Davies & Gibling (2010) have documented the profound effect that this botanical revolution had on river systems, and thus on sedimentological styles and preservation of evidence of the activity of the fledgling terrestrial biota. With the establishment of complex plant ecosystems during the Devonian, and their accompanying growth of extensive root systems, river systems changed from braided, laterally expansive outflows to constrained water flow in well-defined channels, with the trapping of finer, muddy fractions on alluvial floodplains. However, there is ample evidence to indicate that prior to the expansion of vascular plants, a range of invertebrates, and perhaps even vertebrates, had already begun to colonise the land and establish simple, but extensive, freshwater and subaerial ecosystems.

There are a number of contenders for pre-Silurian colonisation of the land by invertebrates, although whether these represent the establishment of nascent ecosystems, or just chance excursions onto land, is not clear. Kennedy & Droser (2011) suggested that as early as the beginning of the Cambrian, in the Wood Canyon Formation in California, millimetre-sized vertical burrows attributed to Arenicolites and Skolithos, along with the centimetre-scale horizontal burrow Psammichnites, were formed in fluvial channels. However, Davies & Gibling (2012) and McIlroy (2012) have argued against a non-marine depositional environment for these sediments, considering rather that the sediments were deposited in a marginal marineinfluenced setting. More convincing evidence for subaerial trackways made by arthropods is found in Upper Cambrian to Lower Ordovician colian dunes of the Nepean Formation in Ontario. These arthropods, attributed unconvincingly to euthycarcinoids, may have been making brief forays on to land, but not been part of any established terrestrial ecosystem.

Two Late Ordovician trace-fossil occurrences have been promoted as providing evidence of the activity of invertebrates in a non-marine environment. On the basis of trace fossils and paleosols, Retallack & Feakes (1987) and Retallack (2001) suggested that the Late Ordovician Juniata Formation in the eastern United States represents an early terrestrial ecosystem, with the dominant elements being burrowing millipedes that fed on nonvascular plants. Davies et al. (2010) have questioned this interpretation, arguing that there is insufficient evidence to ascribe the burrows to formation by millipedes, no evidence for plant material, and that the sediments could equally well be interpreted as having been deposited in a marginal marine environment. Trackways made by arthropods have been described from the Late Ordovician Borrowdale Volcanic Group in the English Lake District. These tracks, made on a wet, but subacrial, sand surface, are indicative, the authors consider, of periodic excursion by myriapod-like arthropods on to the land (Johnson et al. 1994).

None of these examples provide any convincing evidence for having been part of an established terrestrial or freshwater ecosystem. Such evidence would include not only a variety of subaerially formed trackways, whether made by invertebrates or vertebrates, but also indisputable living and feeding burrows preserved in

sediments deposited either by fluvial or eolian agencies. Herringshaw & Solan (2008) have pointed out that recognising the first evidence for the colonisation of infaunality in shallow-marine environments, the colonisation of deep sea habitats and the colonisation of freshwater ecosystems in the terrestrial environments all come in the form of bioturbation. While our knowledge of the history of bioturbation in marine settings is well established, in the freshwater it is not. As Herringshaw & Solan (2008) have observed, the dwelling burrows that occur in the Tumblagooda Sandstone probably represent the earliest examples of such burrows. That, combined with a wide range of other dwelling burrows, hunting burrows, tracks and trails, point to the Tumblagooda Sandstone trace-fossil fauna as probably providing evidence of the oldest known establishment of relatively sophisticated trophic systems within a terrestrial freshwater ecosystem, in the early to mid-Silurian. This is contrary to the assertions of Buatois et al. (1998) and Buatois & Mángano (2011) that such ecosystems did not become established on land until the Silurian - Devonian boundary, penecontemporaneous with the evolution and rapid expansion of vascular plants. Assuming that Trewin's (1993a, b) freshwater hypothesis is correct, what the Tumblagooda Sandstone trace fossils indicate is that an arthropod-dominated terrestrial ecosystem predated the evolution of vascular plants, being present by the mid-Silurian.

ACKNOWLEDGEMENTS

I am indebted to my family, Sue Radford, Jamie McNamara, Katie McNamara and Tim McNamara for helping me so much in the field, for many years, and for often finding the best new trace fossils. Kris Brimmell, discoverer of her euthycarcinoid, has been an immense help over the years, both in the field, and with photography. Nigel Trewin, who did much of the work on the sedimentology and trace fossils is especially thanked, as are the various rangers of Kalbarri National Park, especially Mike Paxman, who facilitated my fieldwork. Thanks also to others who helped in the field, particularly Duncan Friend. I am very grateful for the help, advice and sage wisdom offered by Roger Hocking on this manuscript, and to Kate Trinjastic for her helpful comments.

REFERENCES

Bradoy S J & Dunlop J A 1997. The functional morphology of mating in the Silurian eurypterid, Baltoeurypterus tetragonophthalmus (Fischer, 1839). Zoological Journal of the Linnean Society 120, 435–461.

Braoshaw M A 1981. Paleoenvironmental interpretations and systematics of Devonian trace fossils from the Taylor Group (lower Beacon Supergroup), Antarctica. New Zealand Journal of Geology & Geophysics 24, 615–652.

Buatois L A & Mángano M G 1993. Ecospace utilization, paleoenvironmental trends and the evolution of early nonmarine biotas. *Geology* **21**, 595–598.

Buatois L A & Mángano M G 1995. The paleoenvironmental and paleoecological significance of the lacustrine *Mermia* ichnofacies: an archetypical subaqueous nonmarine trace fossil assemblage. *Ichnos* 4, 151–161.

BUATOIS L A & MÁNGANO M G 2004. Animal-substrate

- interactions in freshwater environments: applications of ichnology in facies and sequence stratigraphic analysis of fluvio-lacustrine successions. *In*: Mcllroy D (ed.) *The application of ichnology to palaeoenvironmental and stratigraphic analysis*, pp. 311–333. Geological Society of London Special Publication 228.
- Buatois L A & Mángano M G 2011. Ichnology: organism-substrate interactions in space and time. Cambridge University Press, Cambridge.
- BUATOIS L A, MÁNGANO M G, GENISE J F, & TAYLOR T N 1998. The ichnologic record of the invertebrate invasion of nonmarine ecosystems: evolutionary trends in ecospace utilization, environmental expansion, and behavioral complexity. *Palaios* 13, 217–240.
- Buckman J O 1996. *Heimdallia* from the Lower Carboniferous of Ireland: *H. mullaghmori* a new ichnospecies, and reevaluation of the three-dimensional format of the ichnogenus. *Ichnos* 5, 43–51.
- Byrne D R & Harris L B 1993. Structural controls on the basemetal vein deposits of the Northampton Complex, Western Australia. *Ore Geology Reviews* 8, 89–115.
- CAWOOD P A & NEMCHIN A A 2000. Provenance record of a rift basin: U/Pb ages of detrital zircons from the Perth basin, Western Australia. Sedimentary Geology 134, 209–234.
- CHISHOLM J I 1985. Xiphosurid burrows from the Lower Coal Measures (Westphalian A) of west Yorkshire. *Palaeontology* 28, 619–628.
- COLLETTE J H, GASS K C & HAGADORN J W 2012. Protichnites eremita unshelled? Experimental model-based neoichnology and new evidence for a euthycarcinoid affinity for this ichnospecies. Journal of Paleontology 86, 442–454.
- COTTER E 1978. The evolution of fluvial style, with special reference to the central Appalachian Paleozoic. *In Miall A D* (ed.) *Fluvial Sedimentology*, pp. 361–384. Canadian Society of Petroleum Geologists Memoir 5.
- DAVIES N S & GIBLING M R 2010. Cambrian to Devonian evolution of alluvial systems: the sedimentological impact of the earliest land plants. *Earth-Science Reviews* 98, 171–200.
- DAVIES N S & GIBLING M R 2012. Early Cambrian metazoans in fluvial environments, evidence of the non-marine Cambrian radiation: comment. *Geology* 40, 270.
- DAVIES N S, RYGEL M C & GIBLING M R 2010. Marine influence in the Upper Ordovician Juniata Formation (Potters Mills, Pennsylvania): implications for the history of life on land. Palaios 25, 527–539.
- Evans R, Mory A J & Tait A M 2007. An outcrop gamma ray study of the Tumblagooda Sandstone, Western Australia. Journal of Petroleum Science & Engineering 57, 37–59.
- FAYERS S R, TREWIN N H & MORRISSEY L 2010. A large arthropod from the Lower Old Red Sandstone (Early Devonian) of Tredomen Quarry, south Wales. *Palacontology* **53**, 627–643.
- Frey R W & Pemberton S G 1984. Trace fossil facies models *In:* Walker R G (ed.) *Facies models* (2nd edition), pp. 189–207. Geoscience Canada Reprint Series 1.
- FREY R W & PEMBERTON S G 1987. The *Psiloniclinus* ichnocoenose, and its relationship to adjacent marine and nonmarine ichnocoenoses along the Georgia coast. *Bulletin of Canadian Petroleum Geology* 35, 333–357.
- FREY R W, PEMBERTON S G & FACERSTROM J A 1984. Morphological, ethological, and environmental significance of the ichnogenera Scoyenia and Ancorichnus. Journal of Paleontology 58, 511–528.
- GORTER J D, NICOLL R S & FOSTER C B 1994. Lower Palaeozoic facies in the Carnarvon Basin, Western Australia: stratigraphy and hydrocarbon prospectivity. *In*: Purcell P G & Purcell R R (eds) *The sedimentary basins of Western Australia*, pp. 373–396. Proceedings of Petroleum Exploration Society of Australia Symposium, Perth.
- Hanken N-M & Stormer L. 1975. The trail of a large Silurian eurypterid. Fossils & Strata 4, 255–270.

- HERRINGSHAW L G & SOLAN M 2008. Benthic bioturbation in the past, present and future. *Aquatic Biology* 2, 201–205.
- HOCKING R M 1979. Sedimentology of the Tumblagooda Sandstone (Silurian) in the lower Murchison River area, Western Australia: a preliminary interpretation. Geological Survey of Western Australia Annual Report for 1978, 40–44.
- HOCKING R M 1981. The Tumblagooda Sandstone, Western Australia: its type section and sedimentology. *Geological Survey of Western Australia Annual Report for 1980, 53–61.*
- HOCKING R M 1991. The Silurian Tumblagooda Sandstone, Western Australia. Geological Survey of Western Australia Report 27.
- HOCKING R M 2000. Geology of the southern Carnarvon Basin. Geological Survey of Western Australia Record 2000/10.
- HOCKING R M & MORY A J 2006. Geology of the Kalbarri area a field guide. Geological Survey of Western Australia Record 2006/19.
- HOCKING R M, MOORS H T & VAN DE GRAAFF W J E 1987. Geology of the Carnarvon Basin, Western Australia. Geological Survey of Western Australia Bulletin 133.
- IASKY R P, MORY A J & SHEVCHENKO S I 1998 A structural interpretation of the Gascoyne Platform, southern Carnarvon Basin, WA. In: Purcell P G & Purcell R R (eds) The sedimentary basins of Western Australia, pp. 589–598. Proceedings Petroleum Exploration Society of Australia, Western Australian Basins Symposium, Perth.
- JOHNSON E W, BRIGGS D E G, SUTHREN R J, WRIGHT J L & TUNNICLIFF S P 1994. Non-marine arthropod traces from the subaerial Ordovician Borrowdale Volcanic Group, English Lake District. *Geological Magazine* 131, 395–406.
- Kennedy M J & Droser M L 2011. Early Cambrian metazoans in fluvial environments, evidence of the non-marine Cambrian radiation. *Geology* 39, 583–586.
- LIBBY W G & DE LAETER J R 1998. Biotite Rb-Sr age evidence for Early Palaeozoic tectonism along the cratonic margin in southwestern Australia. Australian Journal of Earth Sciences 45, 623-632.
- LONG J A & GORDON M S 2004. The greatest step in vertebrate history: a paleobiological review of the fish-tetrapod transition. *Physiological and Biochemical Zoology* 77, 700–719.
- MCLLROY D 2012. Early Cambrian metazoans in fluvial environments, evidence of the non-marine Cambrian radiation: comment. *Geology* 40, 269.
- McNamara K J & Trewin N H 1993. A euthycarcinoid arthropod from the Silurian of Western Australia. *Palacontology* **36**, 319– 335
- MORRISSEY L B & BRADDY S J 2004. Terrestrial trace fossils from the Lower Old Red Sandstone, southwest Wales. *Geological Journal* 39, 315–336.
- MORY A J, NICOLL R S & GORTER J D 1998. Lower Palaeozoic correlations and thermal maturity, Carnarvon Basin, WA. In: Purcell P G & Purcell R R (eds) The sedimentary hasins of Western Australia, pp. 599–611. Proceedings Petroleum Exploration Society of Australia, Western Australian Basins Symposium, Perth.
- Nemchin A A & Pidgeon R T 1999. U-Pb ages on titanite and apatite from the Darling Range granite: implications for Late Archean history of the southwestern Yilgarn Craton. *Precambrian Research* 96, 125–139.
- NETTO R G 2007. Skolothos-dominated piperock in nonmarine environments: an example from the Triassic Caturrita Formation, southern Brazil. In: Bromley R G, Buatois L A, Mángano G, Genise J F & Melchor R N (eds) Sediment-organism interactions: a multifaceted ichnology, pp.109–121. SEPM Special Publication 88.
- Niedźwiedzki G, Szrek P, Narkiewicz K, Narkiewicz M & Ailberg P E 2010. Tetrapod trackways from the early Middle Devonian period of Poland. *Nature* 463, 43–48.
- OGG J G, OGG G & GRADSTEIN F M 2008. The Concise Geologic Time Scale. Cambridge University Press, Cambridge.

- ÖPIK A A 1959. Tumblagooda Sandstone trails and their age. Bureau of Mineral Resources Report 38, 3–20.
- PHILIP G M 1969. Silurian conodonts from the Dirk Hartog Formation, Western Australia. Proceedings of the Royal Society of Victoria 82, 287–297.
- RETALLACK G J 2001. Scoyenia burrows from Ordovician palaeosols of the Juniata Formation in Pennsylvania. Palaeontology 44, 209–235.
- RETALLACK G J 2009. Cambrian, Ordovician and Silurian pedostratigraphy and global events in Australia. *Australian Journal of Earth Sciences* 56, 571–586.
- RETALLACK G J & FEAKES C R 1987. Trace fossil evidence for Late Ordovician animals on land. *Science* 235, 61–63.
- RICHARDS J R, BLOCKLEY J G & DE LAETER J R 1985. Rb-Sr and Pb isotope data from the Northampton Block, Western Australia. Bulletin and Proceedings of the Australasian Institute of Mining and Metallurgy 290, 43-55.
- Scheel M, Seemann, R, Brinkmann M, Di Michiel M, Sheppard A, Breidenbach B & Herminghaus S 2008. Morphological clues to wet granular pile stability. *Nature Materials* 7, 189–193.
- Schliff M 2011. A new classification concept for U-shaped spreite trace fossils. Neues Jahrbuch für Paläontologie Abhandlungen 260, 33–54.
- Schmidt P W & Embleton B J J 1990. The palaeomagnetism of the Tumblagooda Sandstone, Western Australia: Gondwana palaeozoic [sic] apparent polar wandering. *Physics of the Earth and Planetary Interiors* 64, 303–313.
- SCHMIDT P W & HAMILTON P J 1990. Palaeomagnetism and the age of the Tumblagooda Sandstone, Western Australia. Australian Journal of Earth Sciences 37, 381–385.
- Seilacher A 1963. Lebensspuren und Salinitäts-Fazies-Symposium zur Unterscheidung mariner und nicht-mariner

- Sedimente, Düsseldorf 1962. Fortschritte in der Geologie von Rheinland und Westfalen 10, 81–94.
- Seilacher A 1967. Bathymetry of trace fossils. Marine Geology 5, 413–428.
- SEILACHER A 1985. Trilobite palaeobiology and substrate relationships. Transactions of the Royal Society of Edinburgh: Earth Sciences 76, 231–237.
- TREWIN N H 1993a. Mixed aeolian sandsheet and fluvial deposits in the Tumblagooda Sandstone, Western Australia. *In*: North C P & Prosser D J (eds) *Characterisation of fluvial and aeolian reservoirs*, pp 219–230. Geological Society of London Special Publication 73.
- Trewin N H 1993b. Controls on fluvial deposition in mixed fluvial and aeolian facies within the Tumblagooda Sandstone (Late Silurian) of Western Australia. *Sedimentary Geology* 85, 387–400.
- TREWIN N H & McNamara K J 1995. Arthropods invade the land: trace fossils and palaeoenvironments of the Tumblagooda Sandstone (?late Silurian) of Kalbarri, Western Australia. Transactions of the Royal Society of Edinburgh 85, 177–210.
- Veevers J J, Saeed A, Belousova E A & Griffin W L 2005. U-Pb ages and source composition by Hf-isotope and trace-element analysis of detrital zircons in Permian sandstone and modern sand from southwestern Australia and a review of the paleogeographical and denudational history of the Yilgarn Craton. Earth-Science Reviews 68, 245–279.
- Woolfe K I 1990. Trace fossils as paleoenvironmental indicators in the Taylor Group (Devonian) Antarctica. *Palaeogeography, Palaeoclimatology & Palaeoecology* 80, 301–310.

Received 8 June 2013; accepted 30 August 2013

Devonian vertebrates from the Canning and Carnarvon Basins with an overview of Paleozoic vertebrates of Western Australia

K TRINAJSTIC 1°, B ROELOFS 2, C J BURROW 3, J A LONG 4.5 & S TURNER 3

- ¹ TIGeR/Applied Chemistry, Curtin University, WA 6102, Australia.
- ² Department of Geology, Curtin University, WA 6102, Australia.
- ³ Queensland Museum, Ancient Environments, 122 Gerler Road, Hendra, Qld 4011, Australia.
- ⁴ School of Biological Sciences, Flinders University, POB 2100, Adelaide, SA 5001, Australia.
- ⁵ Museum Victoria, PO Box 666, Melbourne, Vic 3001, Australia.
- * Corresponding author 🖾 K.Trinajstic@curtin.edu.au

A diverse vertebrate fauna, comprising both micro- and macrovertebrate remains, is known from the Paleozoic of Western Australia. However, it is the Late Devonian fauna of the Gogo Formation that shows exceptional preservation and which is the best known. Advances in tomographic techniques, both micro-CT and synchrotron, have revealed new histological data providing information on bone growth, muscle attachments and the evolution of teeth. The fishes from the Gogo Formation have also revealed new information on the evolution of reproductive structures and live birth in early vertebrates. Recent work on the Frasnian reefs that crop out along the Lennard Shelf and mineral drillcore through Paleozoic sedimentary rocks have yielded scales of agnathan thelodonts, and the bones, teeth and scales of sharks, acanthodians and osteichthyans, all of which have increased our knowledge of Ordovician-Late Devonian microfaunas in the Canning Basin, contributing to our understanding of biostratigraphy and correlation within Australia and globally. Less work has been undertaken in the Carnarvon Basin, although like the Canning Basin this has concentrated on Late Devonian strata. More recently, work has commenced on describing Early Carboniferous faunas from the Canning, Carnarvon and Bonaparte Basins. All this work is providing information on faunal patterns and exchange of vertebrates through the Paleozoic. However, the paleogeographic evidence provided by the vertebrates is sometimes at odds with paleogeographic reconstructions based on paleomagnetic evidence and further investigation is required to resolve these differing interpretations.

KEYWORDS: biostratigraphy, early vertebrates, East Gondwana, Lagerstätten, paleogeography, Paleozoic.

INTRODUCTION

Paleozoic fossil fishes of Western Australia, particularly those from the Gogo Formation Lagerstätten located in the Canning Basin, have been invaluable for investigating major evolutionary transitions due to the exceptional preservation and diversity of the fauna. The gnathostomes (jawed vertebrates) recovered from the Gogo Formation in the Kimberley region comprise members of all the major groups and demonstrate key evolutionary shifts from the development of jaws and teeth, the first expression of live-young bearing in vertebrates, to the emergence of stem tetrapods. However, and unlike many other sites in the State, to date no jawless vertebrates have been recovered from this site. In contrast to the excellent preservation found in the fossils of the Gogo Formation, those from the more southerly Carnarvon Basin are disarticulated but show high faunal diversity.

In Western Australia the fossil record of Paleozoic fishes includes both microvertebrate and macrovertebrate remains (Long & Trinajstic 2000, 2010; Burrow *et al.* 2010). The majority of the research conducted to date has been on Devonian, especially Late Devonian marine faunas, with studies on Ordovician, Silurian,

Carboniferous and Permian fossils less common. There are no reports of Cambrian vertebrate fossils from Western Australia, although rare, purported vertebrate fossils of this age are known from deposits in central Australia (Young et al. 1996). Studies on Western Australian Ordovician to Early Devonian taxa are restricted to microvertebrate faunas recovered from mineral drillcore. However, the extensive outcrops of Devonian reefs in the Canning Basin are rich in both macro- and microvertebrate faunas and numerous studies on both have been undertaken.

the early 20th century predominantly morphological descriptions and taxonomic studies were undertaken. In the latter part of the 20th century research began to focus on biostratigraphy, particularly in the areas of marine-non-marine correlation under the UNESCO: IUGS IGCP328 Paleozoic Microvertebrates project led by Alain Blieck, Susan Turner and Gavin Young (Blieck & Turner 2000). Unlike many of the currently used invertebrate zone fossils including conodont elements, Paleozoic fish often occur in transitional environments, with the same species inhabiting marine, nearshore and/or non-marine facies. Some marine units bearing microvertebrates are extremely well dated through tying the vertebrate faunas to standard conodont zonations (Trinajstic & George 2009). In continental rocks microvertebrates are often the only age indicators preserved. Since 1980 there has been a systematic effort to recover microvertebrate remains from Gondwanan Paleozoic rocks from Australia and neighbouring countries (Long 1990; Turner 1982a, b, 1991, 1993, 1997; Vergoossen 1995; Young 1986, 1987; Basden *et al.* 2000; Young & Turner 2000; Burrow 2002; Macadie 2002; Burrow *et al.* 2010; Young *et al.* 2010).

Morphological studies of macrovertebrates have recently taken the forefront again with the advent of new computerised tomographic techniques, allowing for the first time non-destructive histological 'sectioning' of dermal plates and *in situ* teeth and scales at high resolution. The fossils from the Gogo Formation have been significant in the utilisation of these new technologies in answering questions on the evolution and development of teeth (Rücklin *et al.* 2012) and scales (Qu *et al.* 2013a, b), muscle attachments to bone (Sanchez *et al.* 2012, 2013), soft tissue preservation (Trinajstic *et al.*2013) and reproduction in vertebrate animals (Long *et al.* 2008, 2009; Ahlberg *et al.* 2009; Trinajstic & Johanson 2014; Trinajstic *et al.* in press a).

Knowledge of the diversity and stratigraphy of vertebrate faunas from the three Paleozoic basins in Western Australia is variable, with some faunas, e.g. the Gogo fauna, having been more studied than others, e.g. the Moogooree Limestone and Utting Calcarenite faunas. However, recent research has given greater insights into the diversity, taxonomy, phylogeny and biogeographic relationships of the Western Australian faunas and

indicates differences from the longer-studied faunas in central and eastern Australia.

CANNING BASIN

The Paleozoic Canning Basin is characterised by deposition of fine-grained marine clastics and carbonates on extensive carbonate platforms and marine shelves (Cadman *et al.* 1993). Vertebrate fossils are known from Ordovician to Carboniferous sedimentary rocks. One of the most studied areas is the Upper Devonian reef complexes, which are well exposed along the Lennard Shelf and form a belt ~350km long and up to 50km wide (Hocking *et al.* 2008). However, the units can be discontinuous at times, narrow and devoid of complete sections due to margin collapse, as is evident in the Napier Range (Shen *et al.* 2008).

The Frasnian strata of Western Australia, especially those in the Canning Basin, have had more numerous studies undertaken on them than those in other areas and ages, yielding a variety of macro- and microvertebrate fossils (Long 1993). The strata are divided into a number of formations representing different reef facies, some of which are laterally equivalent. For example, the contemporaneous Gogo, Sadler and Pillara formations represent basinal, slope and backreef facies, respectively (Playford *et al.* 2009).

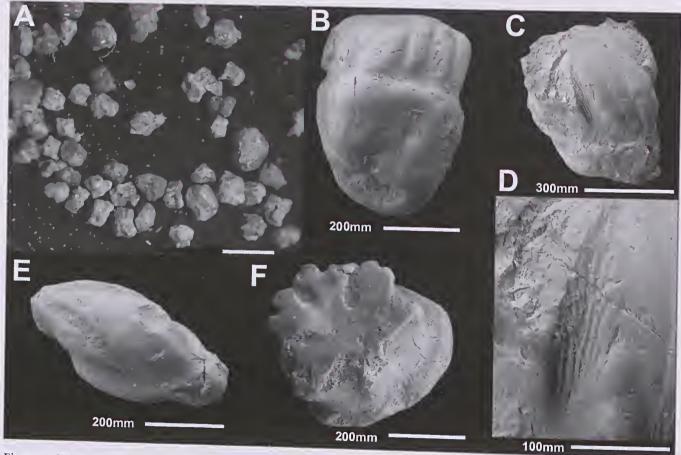


Figure 1 Thelodont scales from Wilson Cliffs 1, Kidston Sub-basin. (A) Isolated scales with grains of quartz attached. (B) Eroded head scale in lateral view. (C) Body scale in anterior view showing linear microornament. (D) Detail of microornament. (E) Body scale in lateral view. (F) Head scale in crown view.

The best known of these in respect to vertebrate fauna is the early Frasnian Gogo Formation, which represents the basinal facies of the reef complex (Long & Trinajstic 2010). This fauna is represented exclusively by macroremains.

The Virgin Hills Formation extends from the lower Frasnian to the uppermost Famennian and represents both basinal and reef slope facies (Playford *et al.* 2009). Rare macrovertebrate remains, mostly of isolated placoderm plates, have been recovered from the Famennian part of the measured section whereas microvertebrates are common from the Frasnian and Famennian reef-slope facies (Trinajstic & Long 2009; Hansma *et al.* in press).

VERTEBRATE FOSSILS OF THE CANNING BASIN

Ordovician

The first description of an Ordovician fish from the Canning Basin was based on fragmentary dermal armour in core recovered from Kidson 1 well, attributed to a new genus and species of arandaspid (jawless fish) *Ritchieichthys nibili* (Sansom *et al.* 2013). Prior to this discovery, reports of Ordovician vertebrate taxa from Australia, including remains from Early to mid-Ordovician, were restricted to marginal marine deposits in central and southeast Australia (Ritchie & Gilbert-Tomlinson 1977; Young 1991, 1997, 2009). Arandaspid

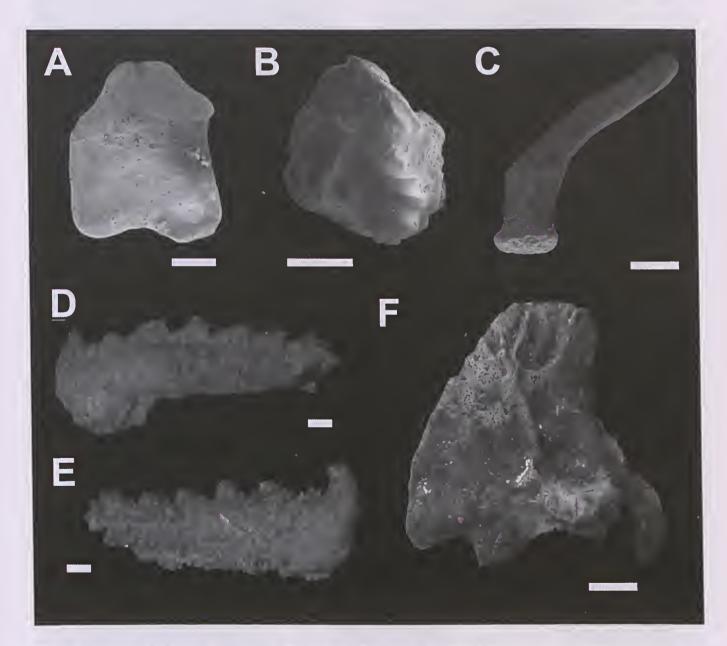


Figure 2 Givetian vertebrate remains from the Cadjebut Formation, Canning Basin. (A) Chondrichthyan tooth gen. et sp. indet., in labial view. (B) Chondrichthyan scale in crown view. (C) Placoderm neural spine. (D, E) Arthrodire infragnathal biting division; (D) left lateral view, (E) right lateral view. (F) Ptyctodont left preorbital plate in visceral view. Scale bar: 0.5 mm in A–C; 0.1 mm in D–E; 5 mm in F.

fishes are also known from central South America (Bolivia) (Gagnier et al. 1996) and Oman in the Arabian peninsula (Sansom et al. 2009) indicating a perigondwanan distribution in a narrow, nearshore environment. This is part of the Gondwanan Evolutionary Assemblage of Blieck & Turner (2003) and Turner et al. (2004).

Silurian

Fossil vertebrates from the Silurian of Western Australia are represented solely by microfossils recovered from boreholes. These primarily comprise thelodont and acanthodian micro-remains with rare scales attributed to actinopterygians. Upper Silurian horizons in Pendock 1A well yielded scales tentatively attributed either to the thelodont *Loganellia* sp. cf. *L. grossi* (V N Karatjute-Talimaa pers comm. 1994) or more probably cf. *Niurolepis* sp. (personal observation ST) and acanthodian *Nostolepis* cf. *alta* and ?stem actinopterygian *Andreolepis*. These taxa suggest correlation with the Late Silurian (Ludlow) in Iran and northern Europe and suggest a relative closeness between northern Gondwana and Laurentia, rather than any massive oceanic barrier at this time.

Upper Silurian horizons in Kempfield 1 yield scales similar in morphology to *Thelodus parvidens* from Avalonia and Laurentia, and in addition those from a possible Silurian Ievel in Gingerah Hill 1 resemble other European loganelliids and *Niurolepis susanae* from Iran, although these have not yet been formally described (Burrow *et al.* 2010; Turner 2014).

There are no known later Ordovician to Early Silurian vertebrates anywhere in Australia probably because of the Hirnantian into Early Silurian glaciation (Turner *et al.* 2004).

Devonian

EMSIAN-EIFELIAN

Early Devonian (late Pragian?-Emsian) scales of the thelodont *Turinia australiensis* (Figure 1A-F) and unnamed acanthodians were described from the Wilson Cliffs 1 borehole (Gross 1971) from the Tandalgoo Red Beds (now named Tandalgoo Formation), a unit underlying the well-known reef complexes of the southern Canning Basin. The recognition of thelodont scales led to the re-dating of the strata from Permian to Early Devonian, demonstrating the utility of microvertebrates in dating rocks in the absence of conodonts, or where conodonts are undiagnostic. The type material was redescribed and refigured by Turner (1995). The assemblage also includes placoderm dermal scales and bone fragments, an onychodont tooth and a

single shallow-marine unidentified conodont element (personal observation, CJB, ST). Turner (1997) reviewed known records of *T. australiensis* in relation to conodont data across Australia.

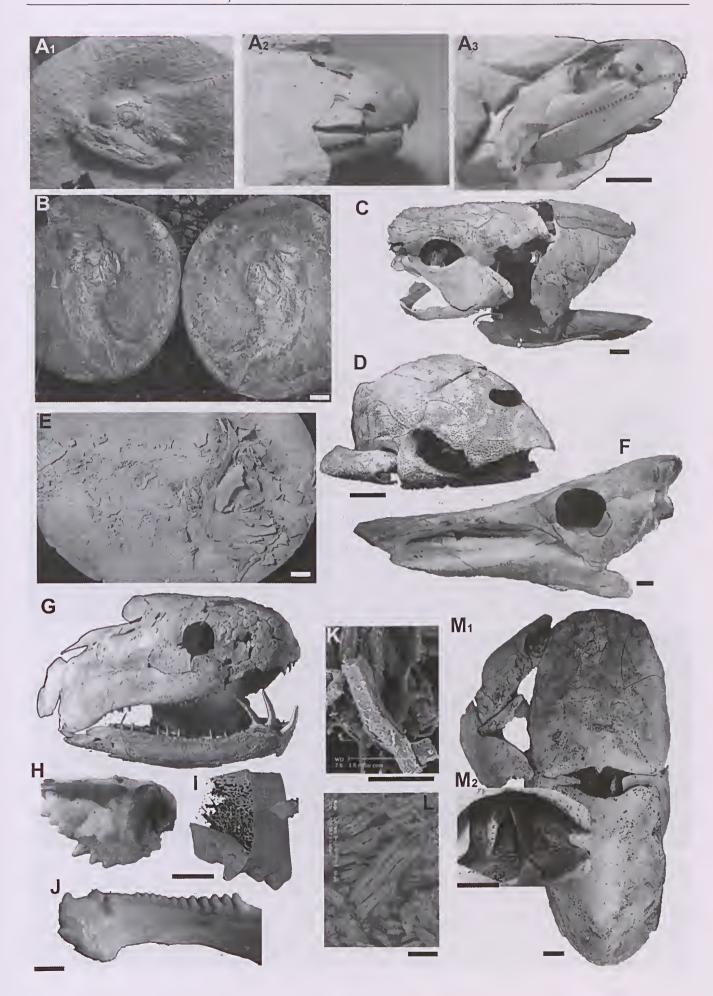
GIVETIAN

The Givetian Cadjebut Formation represents a restricted marine environment and to date only a small number of invertebrate fossils of low diversity have been reported. In 2010 isolated toothplates were recovered by Peter Haines (GSWA) and identified (by KT) as those of a ptyctodont placoderm. Further collecting in 2011 yielded a single chondrichthyan tooth of indeterminate affinity (Figure 2A) and chondrichthyan scales (Figure 2B). Additional 3D-preserved placoderm material was also collected including vertebral elements (Figure 2C), dermal plates and tooth plates (Figure 2D, E) representing new genera and species of arthrodires, and dermal plates from the headshield of a ptyctodont (Figure 2F). Elsewhere in Australia, placoderm remains are common components in Lochkovian to Famennian strata throughout eastern Australia (Young 1993; Parkes 1995; Turner et al. 2000; Burrow 2003), as well as in early Givetian strata in the MacDonnell Ranges of central Australia (Young et al. 1987; Young & Goujet 2003; Young 2005). Their rarity in Lower Devonian strata of Western Australia is possibly a result both of lack of outcrop as well as lack of exploration.

FRASNIAN

The first fishes were collected from the Gogo Formation in the 1940s by Curt Teichert who identified placoderm fossils, which he recognised as being similar in morphology to the European coccosteids (Long 2006). It was not until Harry Toombs from the British Museum (Natural History) (BMNH) visited the University of Western Australia in 1955 and was given material to prepare using his new acetic acid technique that the full extent of this find was realised (Figure 3A1.3). The limestone concretions were found to contain fossils preserved in 3D with the original bones intact and undistorted (Figure 3B). Toombs returned and represented the BMNH in two major expeditions, which systematically collected fish and crustaceans from the Gogo Formation in 1963 and 1967, in collaboration with the Western Australian Museum and Hunterian Museum (Glasgow, Scotland). The Gogo Formation has to date yielded 45 species of fish (Long & Trinajstic 2010), the majority being arthrodire placoderms (25%) (Figure 3C), with antiarchs (10%) (Figure 3D), and ptyctodonts (5%) (Figure 3E), recovered in lesser numbers. Of the osteichthyans, palaeoniscoids (Figures 3B, 5C, D) represent the next most abundant group (24%), followed

Figure 3 Vertebrate remains from the Gogo Formation, Canning Basin. (A_{1,3}) Gogonasus andrewsae head at various stages of acetic acid preparation. (B) A split nodule in the field containing a palaeoniscoid in part and counterpart. (C) Arthrodire Incisoscutum ritchiei head and trunk shield in lateral view. (D) Head and trunk shield of Bothriolepis sp. (E) Austroptyctodus gardineri (counterpart) in lateral view. (E) Head of Griphognathus whitei in lateral view. (G) Onychodus of Compagopiscis croucheri upper toothplate in ventral view. (I) CT scan of upper toothplate of Compagopiscis croucheri showing histological detail; (J) lower toothplate of C. croucheri in lateral view. (K) Mineralised muscle fibres from the arthrodire Incisoscutum ritchiei. (L) Mineralised biofilm surrounding muscle fibres in Eastmanosteus calliaspis. (M) Eastmanosteus calliaspis with nuchal gap musculature preserved; (M₁) detail of nuchal gap musculature.



by dipnoans (20%) (Figure 3F), and osteolepiforms (2%) (Figure 3G). More recently, a single acanthodian was described by Burrow *et al.* (2012). In addition two sharks and a coelacanth have been prepared but await full description. Long & Trinajstic (2010) gave a recent review of the faunal composition and so only a brief overview of discoveries post-2010 will be presented here.

With the advent of new technologies, including micro CT and synchrotron tomography, the first nondestructive examinations of histological structures of the fishes from the Gogo Formation have been undertaken (Long et al. 2008; Sanchez et al. 2013; Trinajstic et al. 2013). The ontogenetic history is largely conserved within the dermal bones preserved as lines of arrested growth (Sanchez et al. 2012, 2013). This characteristic has enabled changes in growth of the jaws to be ascertained and led to significant advances in our understanding of the development of teeth (Figure 3H-J) in some early jawed vertebrates (Smith & Johanson 2003; Rücklin et al. 2012). The presence or absence of teeth in placoderms has been a controversial topic, particularly since the proposition by Smith & Johanson (2003) that teeth were secondarily developed in arthrodire placoderms from 'toothless' ancestors. Synchrotron scans of the jaws of an arthrodire (Compagopsicis) showed the pulp canal within each tooth became infilled during growth (Rücklin et al. 2012). This discovery supports Smith & Johanson's (2003) hypothesis that the dental structures in arthrodires are true teeth, and teeth might have evolved at least twice in early vertebrate evolution. Studies on the antiarch Bothriolepis (Figure 3D) show tooth-like structures on biting surfaces that are consistent with the histology of the dermal armour, further indicating that teeth and jaws may not have evolved simultaneously (Rücklin et al. 2012), as antiarchs are considered to be basal phylogenetically to arthrodires (Zhu et al. 2013)

Reconstructing the soft anatomy of extinct animals has often been a pipe dream in paleontology, and has until recently mostly relied on functional interpretation and the preservation of muscle scars on the skeleton. The interolateral plate (= clavicle) of placoderms was hypothesised to be the site of the coracobranchialis muscle (Johanson 2003). Synchrotron studies of the interolateral plate from Compagopiscis a placoderm from Gogo revealed the presence of numerous embedded extrinsic fibres indicating muscle attachment points. The principal fibre alignments are anteroposterior in the anterior part of the attachment and anterodorsal in the more dorsal part indicating the presence of two muscles (Sanchez et al. 2012), where previously only one muscle had been predicted (Heintz 1930; Miles 1969; Johanson 2003). Changes in the distribution of osteocyte lacunae within the bone indicated where deep enthesis (connective tissue between the tendon and the bone) of tendon-attached muscles formed, often leaving a muscle scar on the external bone, whereas more shallow muscle insertions left no muscle scars (Sanchez et al. 2012). These superficial muscle entheses had not previously been predicted on the basis of visual examination of the bone and so the number of muscles present in these extinct organisms has been underestimated (Trinajstic et al. 2012). Thus not only can the synchrotron reveal the site of muscle attachment but also the type of attachment. This technique, pioneered on Gogo fish, has made the

reconstruction of soft anatomy far more accurate than previously realised.

The exceptional preservation of fossils in the Gogo Formation is not restricted to the preservation of bone but includes mineralised muscles also preserved in 3D, in placoderms, chondrichthyans and palaeoniscoids. Initially only small amounts of muscle were recovered from under the dermal plates of the headshield (Figure 3K, L), which had collapsed onto themselves forming a closed micro-environment providing the condition conducive to soft-tissue preservation (Trinajstic et al. 2007). Low pH and rapid burial were important factors in the preservation of the muscle tissues but recent research on invertebrate taxa from the Gogo Formation has shown that the action of sulfur-reducing bacteria prior to burial was also significant in the mineralisation of soft tissues (Melendez et al. 2013). In some instances individual cells are replicated by a single crystal of apatite, exactly replicating the structure of muscle and nerve fibres (Trinajstic et al. 2007). The recognition that mineralised soft tissues were present in the fossils (vertebrate and invertebrate) from Gogo led to different preparation techniques, reduced concentrations of acid and virtual preparation through synchrotron scanning. Using these techniques nearly all the postcranial musculature in the arthrodire Compagopiscis croucheri and the nuchal gap muscles in Inciscoscutum ritchiei and Eastmanosteus calliaspis (Figure 3M,-M2) have been identified (Trinajstic et al. 2013). The significance of this discovery was that more muscles were found to be present in the neck than originally predicted from studies based on comparative morphology. Although the presence of paired head elevator and depressor muscles was predicted based on functional consideration, the division of the head elevators into medial and lateral muscles had not (Trinajstic et al. 2013). In addition, the presence of the cucullaris muscle, a head depressor muscle presumed to be common to all jawed vertebrates, was confirmed for the first time. A second group of specialised muscles, which had never been predicted, was found to be present in the ventral body wall (Trinajstic et al. 2013). Although their function is yet to be determined, their position at the junction of the trunk armour and the tail suggests that they play a role in minimising shear during tail propulsion (Trinajstic et al. 2013).

Although sexual dimorphism had been recognised in ptyctodonts (Watson 1934, 1938), it was not until the identification of claspers in the ptyctodontid Ctenurella (Ørvig 1960) that the possibility of internal fertilisation in ptyctodonts was suggested (Patterson (1965). In a review of the Scottish ptyctodont Rhamphodopsis, Miles (1967), noted it was impossible at that time to determine whether the mode of copulation in ptyctodonts resulted in oviparity or viviparity. This conundrum was finally solved when a single embryo (Figure 4A) was discovered in the ptyctodontid Materpiscis attenboroughi, which demonstrated beyond doubt the presence of internal fertilisation with live birth almost 200 million years earlier in the fossil record than previously known (Long et al. 2008; Trinajstic et al. 2012). One of the most crucial pieces of evidence in the determination of embryos in placoderms was the presence of the mineralised umbilical cord (Figure 4A) in M. attenboroughi (Long et al. 2008). Following this discovery, three embryos, previously identified as scales, were recorded from *Austroptyctodus gardineri* (Figure 4B) (Long *et al.* 2008). Male claspers had previously been identified by Miles & Young (1977) in *Austroptyctodus* (Figure 4C). Small dermal plates had also been recovered from the abdominal area of an arthrodire *I. ritchiei* (Figure 4D, E), but the absence of any evidence for sexual dimorphism and the honeycomb nature of the bone, which was

originally interpreted as being the result of digestion, meant that these plates were identified as prey items (Dennis & Miles 1981). Comparison with the honeycomb nature of the embryonic plates in the ptyctodonts (Figure 4F) allowed the reinterpretation of the arthrodire plates as embryonic bones (Long *et al.* 2009). The presence of an articulation surface on the pelvic girdle of *Austrophyllolepis*, interpreted as for claspers (Long *et al.* 2009), suggested that sexual dimorphism also occurred

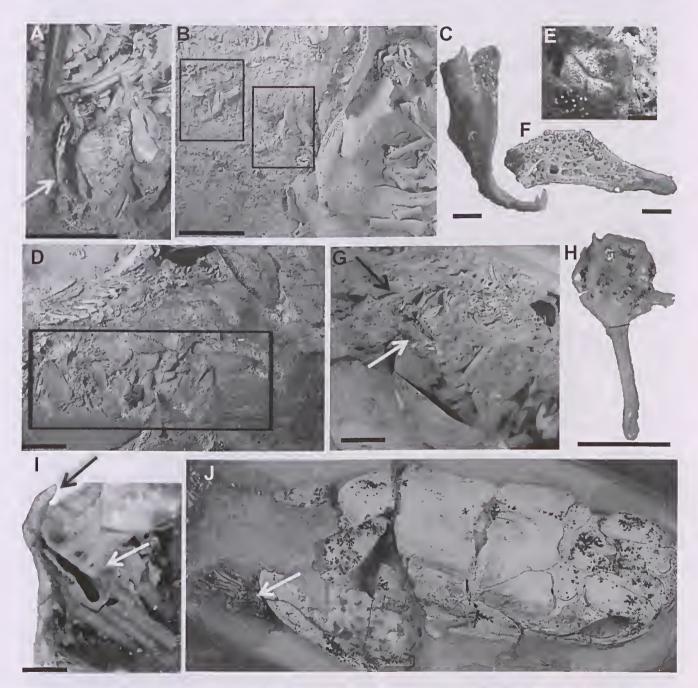


Figure 4 Reproductive structure in placoderms from the Gogo Formation. (A) *Materpiscis* embryo with detail of the mineralised umbilical cord indicated by a white arrow. (B) *Austroptyctodus gardineri*, internal view with 2 embryos within the rectangular outline. (C) Male clasper from *Austroptyctodus gardineri*. (D) Internal view of *Incisoscutum ritchiei* with embryonic bones within the rectangular outline. (E) Close up of embryonic plate from *Incisoscutum ritchiei*. (F) Embryonic plate from *Austroptyctodus gardineri*. (G) Internal view of *Incisoscutum ritchiei* showing male clasper (black arrow) and pelvic girdle (white arrow). (H) Detail of male clasper from *Incisoscutum ritchiei*; (l) close up of male clasper (black arrow) and pelvic girdle (white arrow) in *Incisoscutum ritchiei*. (I) Female specimen of *Compagopiscis croucheri* showing the pelvic girdle (white arrow). Scale bar: 1 cm in A, B, D, G, H, J; 1 mm in C, F; 2 mm in E; 5 mm in I.

in arthrodires. The final piece of the puzzle was revealed with the discovery of a male clasper (Figure 4G–I) in *I. ritcliiei* (Ahlberg *et al.* 2009), which could be distinguished from the pelvic girdle (Figure 4G, I, J) and in *Holonema westolli* (Figure 5A, B) confirming sexual dimorphism with viviparity in ptyctodont and arthrodire placoderms (Trinajstic *et al.* in press a).

Soft tissues have also been recovered in the first and only acanthodian, *Halimacanthodes ahlbergi* described from the Gogo Formation (Burrow *et al.* 2012). The body outline is preserved in the resin-embedded side of the nodule, and was therefore protected during acetic acid preparation. The specimen represents a juvenile, as there is no scale cover in the mid-body region of the fish and there are a low number of growth zones in the scales. These features have been recognised as indicating a juvenile stage from comparison with the ontogenetic series in *Lodeacanthus gaujicus* (Upeniece 1996) from the Frasnian Lode Quarry, Latvia. The Gogo acanthodian shows a close affinity to *Howittacanthus kentoni* from the Frasnian lacustrine mudstones of Mt Howitt, Victoria (Long 1986).

The palaeoniscoid actinopterygians or ray-finned fishes have been revised in recent years by Choo et al. (2009) and Choo (2011), who have extended the actinopterygian faunal list of the site to five taxa, from the original two described by Gardiner (1984). The Gogo actinopterygians also show preserved soft tissues (Figure 5C) and, in rare cases, organs including the gut, gill area and liver (Trinajstic et al. in press b). The anatomical positions of these organs are comparable to those of extant actinopterygians. The path of the intestine is identified, as the cavity where the intestine ran has been infilled with calcite cement. Although this sort of replacement precludes preservation of gut contents (Trinajstic et al. in press b), conodont animals recovered from within the abdominal cavity (Nicoll 1977) and the branchial region (Figure 5D) of two specimens indicate that these fish were carnivores, consistent with the diet indicated by their dentition (Choo et al. 2009).

Most recent work on Gogo lungfishes includes description of new taxa of holodontid lungfishes including *Xeradipterus* (Clement & Long 2010) plus a new species of rhinodipterid, *Rhinodipterus kimberleyensis* (Clement 2012). Clement & Long (2010) also reported the first record of a marine lungfish showing air-breathing adaptations based on a specimen of *Rhinodipterus* from the Gogo Formation with cranial rib articulations on its braincase.

The tetrapodomorph fish *Gogonasus andrewsae* (Long 1985) is now known from several relatively complete specimens (Holland & Long 2009) (Figure 3A). Holland (2013) has recently described the pectoral girdle and fin in detail. Large holes on top of the head are identified as spiracles in this genus and were suggested as accessory breathing structures by Long *et al.* (2006). Recent work on the physiology of the modern air-breathing fish *Polypterus* now confirms that spiracular breathing was common in basal osteichthyans and most likely explains why fish like *Gogonasus* have such large spiracles (Graham *et al.* 2014).

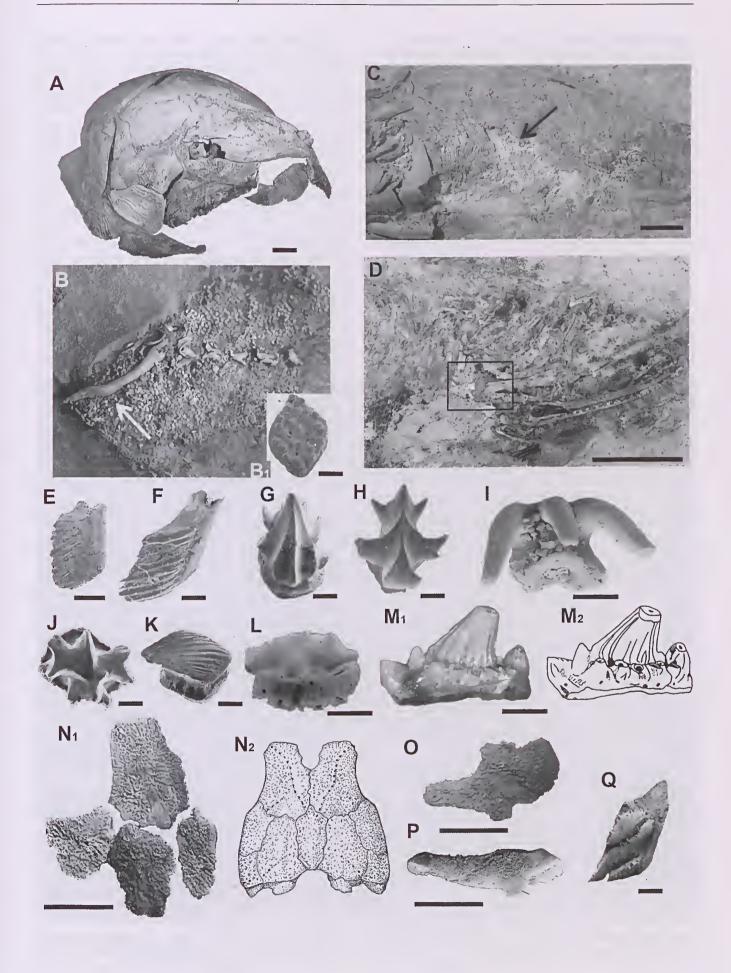
The other important aspect of the exceptional preservation from the Gogo Formation has been the ability to identify and compare isolated scales from the contemporaneous Gneudna Formation, Carnarvon Basin (see below) and the Virgin Hills Formation, Canning Basin. The variation in scale morphology present in palaeoniscoids is exhibited in key features including shape and ornamentation, enabling identification of the body area from which isolated scales originated. Following Esin (1990), different squamation areas in the Gogo palaeonosicoids have been recognised, enabling two species, Moythomasia durgaringa and Mimia toombsi to be identified from the Gneudna Formation (Figure 5E, F) (Trinajstic 1999c, 2000) and scales from M. durgaringa to be identified from the Virgin Hills Formation (Trinajstic & George 2009) and Hull Range (Chow et al. 2013), Canning Basin, providing biostratigraphic constraints for these strata. In addition scales from the placoderm Holonema westolli Miles 1971 (Figure 5B) were also identified in the Gneudna Formation (Figure 5B,) based on the description of a complete tail recovered from the Gogo Formation (Trinajstic 1999a).

As noted above, the Gogo Formation fishes are further contributing important information on reproduction in early jawed fishes, including viviparity as an early vertebrate reproductive strategy, multiple embryos and ontogenetic series, which enable questions of taxonomy, phylogeny and development to be addressed (Johanson & Trinajstic 2014, Trinajstic *et al.* in press b).

VIRGIN HILLS FORMATION: FRASNIAN

The microvertebrate fauna described from a measured section at Horse Spring in the Canning Basin is dominated by the lodont scales (Figure 5G, H) and phoebodont teeth (Figure 5I) with a smaller number of acanthodian and palaeoniscoid scales as well as protacrodont teeth also recovered (Turner 1997; Trinajstic

Figure 5 Vertebrate remains from the Gogo, Virgin Hills and Gneudna Formations. (A) Head shield of Holonema westolli. (B) Body scales and clasper (white arrow) Holonema westolli from the Gogo Formation; (B₁) body scale of Holonema westolli from the Gneudna Formation. (C) Moythomasia durgainga in lateral and internal view showing mineralised soft tissue (white arrow). (D) Gogosardinia with conodont (rectangular outline) in the branchial regions. (E) Moythomasia durgainga type A scale and (F) type B scale from the Gneudna Formation. (G, H) Scales from Australolepis seddoni in crown view Virgin Hills Formation, Horse Spring, Canning Basin. (I) Phoebodus bifurcatus tooth in crown view Virgin Hills Formation, Horse Spring, Canning Basin. (J) Scale from Australolepis seddoni in crown view, Gneudna Formation, Carnarvon Basin. (K) Cheiracanthus sp. body scale in crown view. (L) Phoebodus sp. tooth In crown view, Gneudna Formation. (M₁) Emerikodus tooth in lingual view from the Gneudna Formation; (M₂) line drawing of Emerikodus. (N₁) Head shield plates of Kimbrynaodus from the Gneudna Formation; (N₂) line drawing of reconstruction of the head shield of Kimbrynaodus. (O) Marginal plate in lateral view of Kimbrynaodus from the Gneudna Formation. (P) Lower tooth plate of Kimbrynaodus from the Gneudna Formation. (Q) Palaeoniscoid scale Gogosardinia coatesi in crown view from the Gneudna Formation. Scale bar: 2 cm in A; 1 mm in B, F-M, Q; 2 mm in E; 1 cm in O, N; 5 mm in P.



2000; Trinajstic & George 2009). The discovery by Trinajstic (2000) represented the first record of the thelodont Australolepis seddoni (Figure 5G, H) cooccurring with conodonts and extended the known stratigraphic range to as young as the standard Montagne Noire conodont zone 10 (CZ10 MN) (Trinajstic & George 2009). This thelodont is a useful index fossil that defines the early Frasnian in East Gondwana (Turner 1997). The presence of A. seddoni scales in the Hull Range has confirmed the Frasnian age of back-reef facies, which are difficult to date with conodonts and ammonoids (Chow et al. 2013). The biogeographic range of A. seddoni is now known to have extended westwards along the northern margin of Gondwana with new discoveries in Iran and possibly Poland (Turner et al. 2002; Hairapetian et al. in press).

Numerous small acanthodian scales have also been recovered from the lower beds of the Horse Spring section and their generic morphology and lack of ornament led to them to be placed in open nomenclature (Trinajstic & George 2009). Following the description of Halimacanthodes ahlbergi the scales from Horse Spring have now tentatively been referred to this taxon (Burrow et al. 2012). Smooth-crowned acanthodiform scales are common components in Frasnian strata (Burrow et al. 2010). Other taxa that co-occur in the Virgin Hills and Gogo formations are scales attributed to the palaeoniscoid Moythomasia durgaringa and toothplates from the lungfish Chirodopterus australis.

Teeth of phoebodont sharks (Figure 51) have also been recovered from the Horse Spring section (Trinajstic & George 2009) and can be correlated with the standard phoebodont zonations elsewhere in Australia and worldwide (Young & Turner 2000, Ginter et al. 2010). Although known to have a global (at least Paleotethyan) range, phoebodont taxa had not been recorded in Western Australia until their recovery from conodont residues at Horse Spring (Trinajstic & George 2009). Phoebodonts have proved useful for biostratigraphy in Givetian to Famennian strata (Ginter et al. 2010) and their range into the Famennian has recently been reported in Western Australia (Roelofs et al. 2013).

NAPIER FORMATION: FRASNIAN

Long (1988) recorded a large upper toothplate (supragnathal) of a ptyctodontid placoderm identified as cf. *Campbellodus* sp. from the Napier Formation in the Canning Basin. In addition, a microvertebrate fauna including scales from thelodonts, acanthodians, chondrichthyans and actinopterygians, and teeth from at least three species of stethacanthid and cladodont sharks have been recovered from beds throughout the section at South Oscar Range.

NAPIER FORMATION: FAMENNIAN

One of the earliest records of Famennian aged vertebrate material in the Canning Basin is from Barker Gorge, in the Napier Range. The fossil was collected by H P Woodward in 1906 and identified as: '...a large Devonian fish (new to science) allied to *Coccosteus*' by his father Henry Woodward, then Keeper of Geology at the British Museum (Glauert 1910 p. 112). A Smith Woodward, who took over as Keeper from Henry Woodward (no relation) in 1901, agreed writing: 'The Western Australian Fossil

looks remarkably like a piece of a large Devonian Coccostean, hitherto unknown in the Australian Region' (Glauert 1910 p. 113). Etheridge (1918) described (but did not figure) similar material collected in 1916 by H Basedow from 'near Old Napier Downs homestead' as the stromatoporoid Stromatoporella kimberleyensis. During a study of the stromatoporoids from the reef complexes, Cockbain (1976) re-examined the Woodward and Basedow material and concluded that it was not a stromatoporoid: additional testing including thin sectioning and X-ray diffraction analyses confirmed the original identification as arthrodire bone (R S Miles in Cockbain 1976). The recovery of further vertebrate fossils from the area has been scant, with a single sharks tooth Stethacanthus cf. thomasi recovered from mineral drillcore (NRD103) at Napier Range and a single tooth of Thrinacodus ferox recovered from Napier Range 1 well located east of Chedder Cliffs and dated as Late Famennian (Chow et al. 2004), based on the associated conodont fauna. Vertebrate remains have been recovered in outcrop from Chedder Cliffs, although, with the exception of some incomplete placoderm dermal plates, most are so broken they are impossible to identify. Conodont samples from Barker River have yielded a single pheobodont tooth and some isolated 'ctenacanthid' type scales.

VIRGIN HILLS FORMATION: FAMENNIAN

A single large placoderm, Westralichthys, was recovered from the crepida zone of the Virgin Hills Formation by Curt Teichert and this was subsequently prepared and described by Long (1987). In 2009, Peter Haines identified bone from a large placoderm in a measured section at Casey Falls, from close to where the original specimen was thought to have been recovered. The new specimen was excavated from the rock in 2011 and is currently undergoing preparation. The plates represent the trunk armor of a large dinichthyid and have been tentatively identified as belonging to Westralichthys, but they await formal description. Towards the top of the section there is a breccia where large isolated, but broken, placoderm plates are present. It has not been possible to identify these fragmentary remains but as they occur in a horizon above strata dated by conodonts as mid-Famennian, this confirms a Famennian age for the uppermost beds. Placoderms did not survive the end-Famennian extinction event, and therefore a younger Carboniferous age for the upper part of the section measured at Casey Falls is ruled out.

The measured section at the Casey Falls locality yielded few microvertebrates, mostly shark teeth, with a small number of acanthodian and palaeoniscoid scales. Preliminary work on the shark fauna confirms the presence of phoebodonts, as elsewhere in Australia (Turner 1982b, 1993; Young & Turner 2000). The ramp facies, above the Casey Falls section, is dominated by a diverse shark assemblage, which includes teeth from protacrodontids, stethacanthids, lonchidiids and the phoebodont *Thriuacodus tranquillus*. Numerous palaeoniscoid scales and teeth and lower numbers acanthodian, scales are also present.

Interestingly, thelodonts, phoebodonts and porolepiforms are yet to be recorded from the Gogo Formation, even though these taxa are known from the Frasnian and Famennian Virgin Hills and Napier formations in the Canning Basin. This is probably a reflection of the preferred environments of these fish, with thelodonts typically in shallower marine, marginal marine to freshwater settings (Turner 1997). Phoebodont sharks, apart from one thrinacrodont from the late Mississippian of the USA, are only known from isolated teeth but typically occur in marine rocks (Ginter & Turner 2010).

Carboniferous

There is a major environmental change towards the end of the Famennian with the cessation of reef building; the marine habitats of the Carboniferous period are dominated by carbonate ramps. The end Famennian is also marked by a major extinction event that affected vertebrates and marked the demise of the placoderms (although the number of families was already reduced after the Frasnian/Famennian extinction event) and a major radiation of sharks and actinopterygians, which is reflected in the shallow-water facies of the Laurel Formation in the Canning Basin. Palaeoniscoid remains (teeth, scales and radial bones) and acanthodian scales

dominate the fossiliferous units. Turner (1982a) identified Thrinacodus ferox from Oscar Hill and renamed earlier Lower Carboniferous shark material described by Thomas (1957). Edwards (1997) found teeth of a new Thrinacodus sp. from a trench dug across the Upper Devonian-Lower Carboniferous by Mawson et al. (1988) to obtain conodont data; Ginter & Sun (2007) named this taxon Thrinacodus bicuspidatus and its range is within the basal Tournaisian in China and Western Australia. Recent work (Roelofs et al. 2013) has also uncovered shark teeth, scales and spines from 21 different taxa including Ageleodus sp., Thrinacodus ferox (Figure 6A), Stethacauthus spp., Protacrodus spp., (Figure 6B, E), Deihim mansureae, Cassisodus sp., Helodus spp., Lissodus spp. (Figure 6C, D)., Orodus sp. and a ctenacanthid sp. (Figure 6F). A partial tooth from a large stethacanthid shark is also of note as it bears strong affinities to teeth in a fragmented but 3D preserved partial jaw and palate from a large specimen of Stethacanthus sp. from the Bonaparte Basin (Turner 1991; Turner in Jones et al. 2000; Turner et al. 1994; Burrow et al. 2010). This indicates the presence of large predatory sharks early in the Carboniferous across north Western Australia (Burrow et al. 2010).

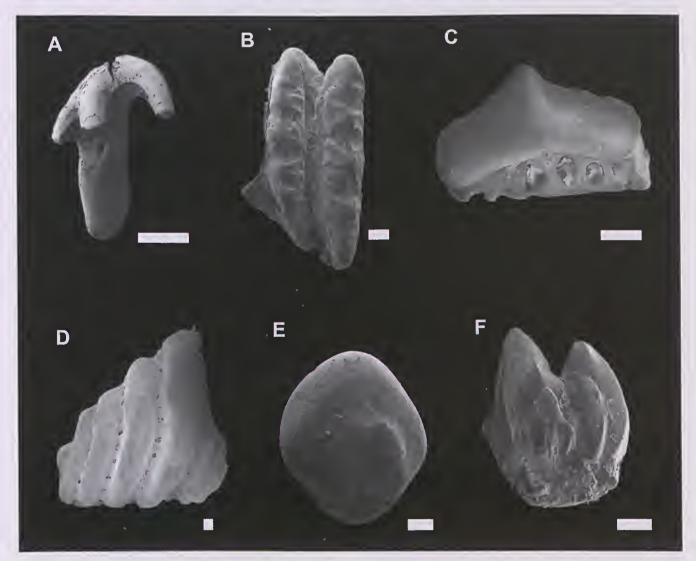


Figure 6 Carboniferous microremains from the Laurel Formation, Canning Basin. (A) *Thrinacodus ferox* tooth in crown view. (B) Partial *Protacrodus* sp. tooth whorl in crown view. (C) *Lissodus* sp. tooth in lingual view. (D) *Lissodus* sp. tooth whorl in crown view. (E) *Protocrodus* sp. scale in basal view. (J) Ctenacanthid scale in crown view. Scale bar: 0.4 mm.

Further work on the diverse shark fauna of the Viséan Utting Calcarenite, Weaber Group, of the Bonaparte Basin has brought to light at least 18 different taxa of eugeneodontid and other sharks as well as sarcopterygian and actinopterygian remains (Chambers 2003; Burrow *et al.* 2010).

Carnarvon Basin

Fish fossils are mostly known only from Late Devonian sediments in the Carnarvon Basin. The early Frasnian Gneudna Formation is interpreted as being deposited along a shallow marine shelf (Hocking et al. 1987). Conformably overlying and interfingering with the Gneudna Formation is the Munabia Sandstone where deposition was initially in a tidal environment grading up to a braided-fluvial system (Moors 1981) with conodonts indicative of marine incursion in the upper part of the section (Nicoll 1979; Hocking et al. 1987). The Frasnian/Famennian boundary occurs within the Munabia Sandstone and the upper part of the section grades into the Famennian Willaraddie Formation, which is at least partly laterally equivalent (Gorter et al. 1998). During the latest Devonian and into the Tournaisian a shallow sea transgressed across the region, reflected by the deposition of the Moogooree Limestone (Hocking 1990). The Permian Byro Group represents cold-water facies, predominantly comprising black shale deposited under anoxic conditions in the outer offshore zone and a lighter coloured shale deposited under less-restricted conditions in the inner offshore zone (Hocking et al. 1987). The changes in bathymetry are thought to reflect tectonic events related to the breakup of Gondwana (Hocking et al. 1987).

Vertebrate fossils of the Carnarvon Basin

Devonian

FRASNIAN

The Gneudna Formation is laterally discontinuous, with most paleontologicial studies (vertebrate and invertebrate) having been concentrated on the type section. The Gneudna type section was described as depauperate in fossil taxa (Dring 1990), however, this statement is only accurate for the invertebrates: the fish fauna is now known to be one of the most diverse marine vertebrate assemblages of this age, with nearly 20 taxa present, the majority of which are represented as microfossils (Turner & Dring 1981; Trinajstic 1999a, b, c; Long & Trinajstic 2000; Trinajstic 2001a, b; Trinajstic & George 2009).

George Seddon (1969) discovered the first vertebrate fossils in conodont residues and determined the remains as either teeth or scales belonging to fish species. Dring (1980) recovered additional fish remains and recorded the presence of placoderms, palaeoniscoids, acanthodians and lungfish; only the thelodonts were formally described following Turner's identification of some of Seddon and Dring's scales, formally described as Australolepis seddoni by Turner & Dring (1981). This was the first evidence of the thelodonts surviving the Givetian/Frasnian extinction event and into the Late Devonian and at the time represented the youngest occurrence of thelodonts in the world. Scales of A. seddoni

(Figure 5J) have been used by Turner (1997) to define the early–mid-Frasnian zone in East Gondwana. So far this species is confirmed from Frasnian deposits CZ 4–10 of the Gneudna and Virgin Hills formations, Western Australia (Trinajstic & George 2009) and eastern Iran (Gholamalian *et al.* 2010).

Following these discoveries, a rich microvertebrate fauna was described that includes additional scales types from Australolepis seddoni, tail scales from the arthrodire Holonema westolli (Figure 5B,), body scales from the palaeoniscoids Mimia gardineri (Figure 5E) and Moythomasia durgaringa (Figure 5F), acanthodian scales recently identified as coming from Homalacanthus alilbergi and Cheiracanthus sp. (Figure 5K), toothplates from the lungfish Chirodipterus australis, porolepiform scales, phoebodont teeth (Figure 5L), and a new genus of shark Emerikodus (Figure 5M, M2). At the time of these descriptions (Trinajstic 2000) the vertebrate fauna was considered far more diverse than that recovered from the Gogo Formation because shark, acanthodian and coelacanths had not yet been discovered in it (Long & Trinajstic 2010). As noted, thelodonts, phoebodonts and porolepiforms are yet to be recorded from the Gogo Formation although these taxa are known from the Frasnian and Famennian Virgin Hills and Napier Formations in the Canning Basin.

In addition to the microvertebrates a small number of macrovertebrates have also been found, with placoderm remains the most common. An anterior dorsolateral plate (WAM 91.4.35), part of the shoulder armour, attributed to the actinolepid placoderm *Groenlandaspis* sp. was identified by Long (1993). Groenlandaspids occur in the Early–Middle Devonian *Wuttagoonaspis* fauna in central New South Wales and the Toomba Range southern Queensland (Ritchie 1973, 1975; Young 1993; Young & Goujet 2003), and right through the Middle and Late Devonian successions throughout Australia. Although common in purported freshwater facies of this age and yet known to have a global occurrence, *Groenlandaspis* has not been reported from the Gogo Formation (Long & Trinajstic 2010).

Other placoderm material comprises plates from the trunk armour and includes a right mesial lateral 2 plate, an anterior ventrolateral plate and an anterior dorsolateral plate of Bothriolepis and a head shield plate (nuchal plate) from the arthrodire Holonenia westolli. The most complete placoderm remains are from the ptyctodont Kimbryanodus described by Trinajstic & Long (2009) (Figure 5N_p, P). The holotype comprises the dermal plates that make up the shoulder girdle and represent the only articulated remains recovered. However, one bed, in the lower part of the section, contains a large number of isolated, but associated plates, including a complete set of dermal head (Figure 5 N1, N2) and trunk shield plates and some endochondral elements of the braincase (Trinajstic & Long 2009). This ptyctodont is one of four species known from Western Australia, the other three occurring in the Gogo Formation. A phylogenetic analysis (Trinajstic & Long 2009) places this taxon as closely related to Materpiscis and Austroptyctodus, both endemic to the Gogo Formation.

Long (1985) referred the lungfish, originally ascribed by Seddon (1969) to *Dipterus* cf. digitatus, to Chirodipterus australis. Many new specimens of isolated lungfish toothplates have been found throughout the section and one partial dipnoan braincase from near the top of the section. Comparisons with the Gogo osteolepiform Gogonasus andrewsae (Long 1985, name amended) show that the Gneudna specimens are significantly larger. Large sigmoid-shaped symphysial teeth and a nearly complete dentary lined with large conical teeth suggest affinity with the genus Onychodus, in particular to Onychodus jaudemarrai from Gogo Formation (Andrews et al. 2006), although the Gneudna species is much larger with more robust teeth (Long & Trinajstic 2000). Isolated rounded scales with regions of small upturned flat tubercles have been referred to an indeterminate porolepiform, with the scales somewhat similar to those of Glyptolepis sp. (Jarvik 1980 figure 178).

The dipnoan genera Chirodipterus and Adololopas, as well as the placoderms Bothriolepis and Holonema, are found in the top of the section, which lies in the falsiovalis conodont zone and has been dated as lower Frasnian. Holonema is represented both in the Gneudna and the Gogo Formations by the species H. westolli (Trinajstic 1999a). The palaeoniscoid species, including scales attributed to juvenile specimens, recorded from the Gneudna and Gogo Formations are Maythomasia durgaringa (Trinajstic 1997b, 1999a, b) and Minia toombsi (Trinajstic 1999c), both species occurring throughout the section. Choo et al. (2009) described three additional palaeoniscoid taxa from the Gogo Formation. One of these, Gogosardina coatesi, has scales with linear ornament, which indicates that the juvenile scales from the Gneudna Formation (Trinajstic 1999b) were misidentified and thus need to be attributed to Gogosardina coatesi (Figure 5Q).

FRASNIAN-FAMENNIAN

A scant macrovertebrate fauna including remains of Bothriolepis sp., Holonema sp. and indeterminate scales of an osteolepiform sarcopterygian was collected from the lowermost outcrops of the Munabia Sandstone and described by Long (1991). These fossils constitute the only record of macrovertebrates from this horizon; however, collecting and processing by CJB in 2011 revealed a similar microvertebrate fauna to the underlying Gneudna Formation. Long (1991) attributed the fauna to a likely Frasnian age based on the similarities in shape and dermal ornament of the Munabia Holonema anterior median ventral plate to the Gogo Holonema westolli plates.

FAMENNIAN

As with the Canning Basin, vertebrate fossils are rare in Famennian strata of the Carnarvon Basin. Within the Willaraddie Sandstone, John Long in 1995 first collected placoderm remains preserved as natural impressions including plates from *Bothriolepis* and a phyllolepid posterior ventrolateral plate. Recently in 2011, Eva Papp (ANU) collected additional phyllolepid plates but these are undiagnostic. Phyllolepids are widespread in the Givetian and younger rocks in Gondwana (around Australia, Antarctica, Turkey, Venezuela) but do not occur until the Late Devonian (Famennian) in the Northern Hemisphere (Europe, Russia, Greenland, North America) following the post-Givetian Laurentia–North

Gondwana collision and thus a Gondwanan origin for the group was proposed by Young (2005).

Carboniferous

The Moogooree Limestone has yielded a rich microvertebrate fauna that has yet to be formally described, although there is a preliminary report (Trinajstic & George 2007). Abundant actinopterygian (palaeoniscoid teeth, radial bones, and scales: Figure 7A) and acanthodian (scales: Figure 7B) remains have been recovered. The chondrichythyan taxa show great diversity with representatives of the Phoebodontidae (Thrinacodus ferox, Thrinacodus bicuspidatus Figure 7C), Protacrodontidae (Deihim mansureae Figure 7D-E, Protacrodus sp.), Stethacanthidae (Stethacanthus sp. Figure 7F), Ctenacanthidae (scales) and Helodontidae (Helodus sp.) present. The diverse shark assemblage shows strong affinities with the Canning Basin shark fauna as well as with faunas from Queensland (Turner 1990; Burrow et al. 2010), South China (Wang & Turner 1995; Ginter & Sun 2007), Morocco (Derycke et al. 2008) and Iran (Hairapetian & Ginter 2009).

Permian

In contrast to eastern Australia (Turner 1993), the Permian record of fossil fishes in Western Australia is sparse, with chondrichthyans the only taxon so far represented. The first shark tooth to be recognised from Permian strata in the Carnarvon Basin comprises 15 teeth arranged along a common spiral root and was designated as Edestus davisii by Woodward (1886). The specimen was collected in the valley of the Arthur River, although as the tooth whorl was not found in situ its exact locality could not be determined. The discovery represented the first record of a novel group of chondrichthyans characterised by the presence of a continuous spiraled tooth whorl. The first description of this unique shark was of Helicopriou bessonowi from the Ural Mountains by Karpinsky (1899) and in his monograph he referred the tooth recovered by Woodward to his new genus Helicoprion. However, Eastman (1902) referred the Western Australian tooth whorl to the genus Campyloprion, which he had erected, and Hay (1909) referred the material to another genus Lissoprion. Controversy remained as to the exact taxonomic affinities of the Western Australian tooth whorl until in 1937 a second specimen comprising 5 teeth was recovered from the bed of the Minilya River near Wandagee Station, although, it too was not in situ. Two years later a third specimen was recovered in situ (Teichert 1940) from the Wandagee Stage (Teichert 1939) [now Wandagee Formation (Condon 1967)] and this new material confirmed the interpretation of Karpinsky (1912) that Woodward's original Western Australian tooth whorl belonged to the genus Helicoprion, and all three specimens were referred to Helicoprion davisii by Teichert (1940).

Helicoprion has a worldwide distribution and its importance in biostratigraphy and correlation was documented early (David & Sussmilch 1931). However, it is the unique morphology of the continuous spiraled tooth whorl and how it functioned that has intrigued scientists the most. Karpinsky (1899) variously reconstructed the spiral tooth whorl at the extreme



Figure 7 Carboniferous microremains from the Moogooree Formation, Carnarvon Basin. (A) Palaeoniscoid scale in crown view. (B) Acanthodian scale in crown view. (C) *Thrinacodus bicuspidatus* tooth in labial view. (D) Stethacanthid sp. Tooth in crown view. (E) *Deilim mansureae* tooth in lingual view. (F) *Deilim mansureae* tooth in labial view. Scale bar: 0.4 mm.

anterior of the upper mouth, on the leading edge of the dorsal fin and even on the tail, although most recent reconstructions show the tooth whorl overhanging the lower jaw (Long 1995). Computerised tomographic scans of the only *Helicopriou* specimen to preserve endoskeletal elements associated with the tooth whorl have revealed that it occupied the complete mandibular arch (Tapinila *et al.* 2013). The largest teeth on the tooth whorl were positioned at the back of the mouth and the shark is interpreted to have eaten soft prey such as squid, using a saw-like motion to slice prey (Tapinila *et al.* 2013).

BIOGEOGRAPHY

Ordovician

The distribution of arandaspids indicates interchange between Australia and South America via northern Gondwana with occurrences in Bolivia, Argentina and Oman as well as central and western Australia (Sansom et al. 2013), with all occurrences in a narrow environmental range in nearshore facies. The Larapinta seaway must have been open between the latter two regions, at least intermittently in the Middle to Late Ordovician to allow dispersal from the Amadeus to the Canning Basin (Blewett 2012).

Silurian

The rare vertebrate faunas recovered from the Silurian of Western Australia show possible affinities with mid to Late Silurian assemblages from Iran, the Baltic and northern Eurasia, and possibly South China (Hairapetian et al. 2008; Burrow et al. 2010; Turner 2014), all in deposits that are also from shallow marine to evaporitic environments. The faunas differ markedly from those of a similar age in southeastern Australia (Burrow et al. 2010). Porosiform poracanthodid remains are found in several of the eastern Australian deposits, but are so far lacking from Western Australia. The only described thelodont known from eastern Australia is a purported turiniid, Turinia fuscina (Turner 1997). This form, however, is similar to that described as Niurolepis susauae in Iran; for now it is best left as ?Turinia fuscina (Burrow et al. 2010). The new Western Australian thelodont(s)

resemble the lodontidid and loganelliid taxa found elsewhere in northern Gondwana and parts of Laurentia; there are possible links also with rare the lodont scales found in Indonesia (Turner *et al.* 1995; Hairapetian & Ginter 2009).

Devonian

EMSIAN

The key taxon of the Wilson Cliffs borehole assemblage, Turinia australiensis (Figure 1A-D), has an interesting transcontinental distribution. In southeastern Australia, all occurrences of Turinia australiensis sensu stricto, both marine and non-marine, are of late Pragian to early Emsian age (Turner 1997). Distribution of T. australiensis and closely related species extends westward from beds referred to the Cravens Peak Formation, western Queensland, from the Mulga Downs Group, Darling Basin, western New South Wales, and Mt Winter beds of the Pertnjara Group, Amadeus Basin, central Australia (Young et al. 1987; Turner 1997), on to the type locality of Wilson Cliffs in the Canning Basin, and other boreholes in Western Australia (Burrow et al. 2010; Turner 2014). These records indicate periodic shallow-water marine incursions of the predominantly non-marine basins of central Australia, following the alignment of the older ephemeral Larapinta seaway.

FRASNIAN

The common vertebrate fauna in the three Paleozoic Basins of Western Australia supports tectonic data indicating a connection, via the North West Shelf, between the Carnarvon and Canning Basins (Stuckmeyer & Totterdell 1992). There are also greater faunal similarities between the marine faunas of Western Australia and those of northern and western Gondwana, consisting primarily of what are now South America, Africa, Iran and the Arabian Peninsula and Armorica than with the faunas of East Gondwana comprising eastern Australia, Antarctica and southeastern parts of China, a pattern similar to that seen with certain invertebrates (Feist & McNamara 2007, 2013; McNamara et al. 2009). This may reflect the fact that the vertebrate faunas of eastern Australia come from predominantly marginal/non-marine facies. However, an alternative hypothesis is that during the early Frasnian, eastern Australia was influenced by different ocean currents, which favoured migration to regions other than Western Australia. Klapper (1989) reported a similar pattern in the biogeographic relationship of conodonts, and concluded that migration of cosmopolitan species (both offshore and nearshore) was affected mainly by oceanic currents. A paleogeographic map indicating the main paleocurrents supports this view (Hairapetian et al. in press), with the coast of Western Australia influenced by different currents than the shores of what is now eastern Australia.

FAMENNIAN-CARBONIFEROUS

The Famennian is characterised by a more cosmopolitan vertebrate fauna (Young *et al.* 2010, Hairapetian *et al.* in press). This is reflected primarily in the occurrence of chondrichthyan taxa common to the Canning, Carnarvon and Bonaparte basins in Western Australia.

CONCLUSIONS

In general, studies over recent decades have increased the known biodiversity of Paleozoic vertebrate taxa from that part of Gondwana that is now Western Australia. Both new exploration and re-study of former drillcores and sites is yielding much new data, which is proving valuable in biostratigraphical studies and understanding of how this part of Gondwana was positioned at that time.

The significance of the macro- and microvertebrate faunas of Western Australia is their remarkable preservation, predominantly 3D, and in the majority of cases showing the fine histological details of the original hard tissues, without recrystallisation or other diagenetic processes obscuring their structure. The exception is the vertebrates from the Famennian Willaraddie Sandstone, where they are preserved as impressions, although 3D latex casts can be made of these. This has allowed significant breakthroughs in understanding of vertebrate faunas in Western Australia. The Gogo Formation area is also now noted as a rich and important contribution to Australian and global geoheritage (Long 2004, 2006; Turner 2009); the astonishing detail of preservation is grounds enough for putting this area forward for World Heritage status.

The recognition of variation in morphology, both ontogenetic and regional variation on articulated macrovertebrate fossils from the Gogo Formation, has made the identification of isolated scales to generic and, in some cases, to species level possible at other sites in Western Australia and globally. This has increased the known range of some taxa and also enabled the greater use of microvertebrate taxa for correlation, and phylogenetic, biostratigraphic and biogeographic studies.

ACKNOWLEDGEMENTS

We would like to thank several people for providing access to collections under their care: Peter Haines & Heidi Johnson (Geological Survey of Western Australia, Perth), Martha Richter (Natural History Museum, London), Mikael Siversson (Western Australian Museum) and David Pickering (Museum Victoria). Thanks to the reviewer Ken McNamara for helpful comments. This work is funded by Australian Research Council (ARC) QEII Fellowship to KT, ARC DP110101127 to KT, and JL, ARC DP 1092870 to KT, CB and JL.

REFERENCES

Ahlberg P, Trinajstic K, Johanson Z & Long J 2009. Pelvic claspers confirm chondrichthyan-like internal fertilization in arthrodires. Nature~460,~888-889.

Andrews M, Long J, Ahlberg P, Barwick R & Campbell K 2006 (for 2005). The structure of the sarcopterygian *Onychodus jandemarrai* n. sp. from Gogo, Western Australia: with a functional interpretation of the skeleton. *Transactions of the Royal Society of Edinburgh Earth Sciences* 96, 197–307.

Basden A, Burrow C J, Hocking M, Parkes R & Young G C 2000. Siluro-Devonian microvertebrates from south-eastern Australia. In: Blieck A & Turner S (eds) Palaeozoic vertebrate biochronology and global marine/non-marine correlation. Final report of IGCP 328 (1991–1996), pp. 201–222. Courier Forschungsinstitut Senckenberg 223.

- BLEWETT R (Editor) 2012. Shaping a Nation: a geology of Anstralia. Geoscience Australia and ANU E Press, Canberra.
- BLIECK A & TURNER S 2000. IGCP 328: Palaeozoic microvertebrates final scientific report Introduction. In: Blieck A & Turner S (eds) Palaeozoic vertebrate biochronology and global marine/nonmarine correlation. Final report of IGCP 328 (1991–1996), pp. 1–67. Courier Forschungsinstitut Senckenberg 223.
- BLIECK A & TURNER S 2003. Global Ordovician vertebrate biogeography. Palaeogeography, Palaeoclimatology, Palaeoccology 195, 37–54.
- Burrow C J 2002. Lower Devonian acanthodian faunas and biostratigraphy of south-eastern Australia. Memoirs of the Association of Australasian Palaeontologists 27, 75–137.
- Burrow C J 2003. Redescription of the gnathostome fauna from the mid-Palaeozoic Silverband Formation, the Grampians, Victoria. *Alcheringa* 27, 37–49.
- Burrow C J, Trinajstic K & Long J 2012. First acanthodian from the Upper Devonian (Frasnian) Gogo Formation, Western Australia. *Historical Biology* 24, 349–357.
- Burrow C J, Turner S & Young G C 2010. Middle Palaeozoic microvertebrate assemblages and biogeography of East Gondwana (Australasia, Antarctica). *Palaeoworld* 19, 37–54.
- CADMAN S J, PAIN L, VUCKOVIC V & LE POIDEVIN S R 1993. Canning Basin, W.A. Bureau of Resource Sciences, Australian Petroleum Accumulations Report 9.
- CHAMBERS B L 2003. Early Carboniferous vertebrate microfossils from the Bonaparte Basin, Northern Australia. MSc thesis, James Cook University, Townsville (unpubl) [not 2002 as in Burrow *et al.* 2010].
- Choo B 2011. Revision of the actinopterygian genus *Mimipiscus* (=*Mimia*) from the Upper Devonian Gogo Formation of Western Australia and the interrelationships of the early Actinopterygii. *Earth and Environemntal Science Transactions of the Royal Society of Edinburgh* 102, 71–104.
- Сноо B, Long J A & Trinajstic K 2009. A new genus and species of basal actinopterygian fish from the Upper Devonian Gogo Formation of Western Australia. *Acta Zoologica* **90**, 194–194.
- Chow N, George A, Trinaistic K & Chen Z Q 2013. Stratal architecture and platform evolution of an early Frasnian syntectonic carbonate platform, Canning Basin, Australia. Sedimentology 60, 1583–1620.
- CLEMENT A 2012. A new species of long-snouted lungfish from the Late Devonian of Australia, and its functional and biogeographical implications. *Palaeontology* **55**, 51–71.
- CLEMENT A & LONG J 2010. Xeradipterus hatcheri, a new dipnoan from the late Devonian (Frasnian) Gogo Formation, Western Australia, and other new holodontid material. Journal of Vertebrate Paleontology 30, 681–695.
- COCKBAIN A E 1976. Stromatoporella kimberleyensis Etheridge Jr. 1918 is a piece of bone. Geological Survey of Western Australia Annual Report for 1975, 133–135.
- Condon M A 1967. The geology of the Carnarvon Basin, Western Australia. Part 2: Permian stratigraphy. Burcan of Mineral Resources Bullctin 77.
- David T & Sussmillen C 1931. Upper Palaeozoic glaciation of Australia: Geology Society of America Bulletin 42, 481–522.
- DENNIS K & MILES R S 1981. A pachyosteomorph arthrodire from Gogo, Western Australia. Zoological Journal of the Linnean Society 73, 213–258.
- Derycke C, Spalletta C, Perri M C & Corradini C 2008. Famennian chondrichthyan microremains from Morocco and Sardinia. *Journal of Paleontology* 82, 984–995.
- DRING R 1980. Palaeobiology of the Gneudna Formation, Late Devonian (Frasnian), Carnarvon Basin, Western Australia. PhD thesis, University of Western Australia, Nedlands (unpubl.).
- EASTMAN C R 1902. On Campyloprion, a new form of Edestus-like dentition. Geological Magazine Dec. 4 v. 9, 148–152.
- EDWARDS A F 1997. Ichthyolith remains from the Devonian-

- Carboniferous Boundary of the Canning Basin, Western Australia. MSc thesis, Macquarie University, Sydney (unpubl.).
- Esin D 1990. The scale cover of *Amblypterina costata* (Eichwald) and the palaeoniscid taxonomy based on isolated scales. *Paleontological Journal* 2, 90–98.
- ETHERIDGE R JR 1918. Observations on Carboniferous and other fossils. In: Basedow H Narrative of an expedition of exploration in northwestern Australia, pp. 250–262. Royal Geographical Society of Australasia, South Australian Branch, Transactions 18.
- Feist R & McNamara K J 2007. Biodiversity, distribution and patterns of extinction of the last odontopleuroid trilobites during the Devonian (Givetian, Frasnian). *Geological Magazine* 144, 777–796.
- FEIST R & McNamara K J 2013. Patterns of evolution and extinction in proetid trilobites during the Late Devonian mass extinction event, Canning Basin, Western Australia. *Palaeontology* **56**, 229–259.
- GAGNIER P-Y, BLIECK A, EMIG C C, SEMPERE T, VACHARD D & VANGUESTAINE M 1996. New paleontological and geological data on the Ordovician and Silurian of Bolivia. *Journal of South American Earth Sciences* 9, 329–347.
- Gardiner B 1984. Relationships of the palaeoniscoid fishes, a review based on new specimens of *Mimia* and *Moythomasia* from the Upper Devonian of Western Australia. *Bulletin of the British Museum of Natural History (Geology)* 37, 173–428.
- GHOLAMALIAN H & KEBRIAEI M R 2008. Late Devonian conodonts from the Hojedk section, Kerman Province, Southeastern Iran. Rivista Italiana di Paleontologia e Stratigrufia, 114, 17–181.
- GINTER M, DUFFIN C & HAMPE O 2010. Chondrichthyes (Paleozoic Elasmobranchii: teeth). *In*: Schultze H-P (ed.) *Handbook of Paleoichthyology, vol. 3D*. Friedrich Pfeil Verlag, München.
- Ginter M & Ivanov A 1992. Devonian phoebodont shark teeth. *Acta Palaeontologica Polonica* 37, 55–75.
- GINTER M & SUN Y 2007. Chondrichthyan remains from the Lower Carboniferous of Muhua, southern China. *Acta Palaeontologica Polonica* 52, 705–727.
- GINTER M & TURNER S 2010. The Middle Palaeozoic selachian genus *Thrinacodus*. *Journal of Vertebrate Paleontology* **30**, 1666–1672.
- GLAUERT L 1910. New fossils from Barker Gorge, Napier Range, Kimberley. Geological Survey of Western Australia Bulletin 36, 111–114.
- GORTER J, MORY A & NICOLL R 1998. Sequence stratigraphy and hydrocarbon potential of the Middle to Upper Devonian (Givetian–Frasnian) sequences in the Carnarvon Basin, Western Australia. In Purcell P C & Purcell R R (eds) The scalimentary basins of Western Australia 2, pp. 450–510. Petroleum Exploration Society of Australia Symposium, Perth, WA, 1998 Proceedings.
- Graham J B, Wegner N C, Miller L A, Jew C J, Lai N-C, Berquist R M, Frank L & Long J A 2014. Spiracular air breathing in polypterid fishes and its implications for aerial respiration in stem tetrapods. *Nature Communications* 5, doi:10.1038/ncomms4022.
- Gross W 1971. Unterdevonische Thelodontier- und Acanthodier-Schuppen aus Westaustralien. *Paläontologische Zeitschrift* 45, 97–106.
- HAIRAPETIAN V, BLOM H & MILLER C G 2008. Silurian thelodonts from the Niur Formation, central Iran. *Acta Palaeontologica Polonica* 53, 85–95.
- HAIRAPETIAN V & GINTER M 2009. Pelagic chondrichthyan microremains from the Upper Devonian of the Kale Sardar section, eastern Iran. *Acta Geologica Polonica* **60**, 357–371.
- HAIRAPETIAN V, ROELOIS B, TRINAJSTIC K & TURNER S (in press) Famennian survivor turiniid thelodonts of North and East Gondwana. *In*: Koenigshof P & Becker T (eds) Devonian climate, sea-level and evolutionary events. *Geological Society of London Special Publication*.

- HANSMA J, TOHVER E, YAN E, TRINAJSTIC K, ROELOFS B, PEEK S, SLOTZNICK S, KIRSCHVINK J, PLAYTON T, HAINES P & HOCKING R (in press) Late Devonian carbonate magnetostratigraphy from the Oscar and Horse Spring Ranges, Lennard Shelf, Canning Basin, Western Australia. Earth and Planetary Science Letters.
- HAY O 1909. On the nature of *Edestus* and related genera, with descriptions of one new genus and three new species. *Proceedings United States National Museum* 37, 43–61.
- Heintz A 1932. The structure of *Dinichthys*: a contribution to our knowledge of the Arthrodira. *In:* Gudger E (ed.) *The Bashford Dean Memorial Volume: Archaic Fishes*, pp. 115–224. American Museum of Natural History, New York.
- HOCKING R M 1990. Carnarvon Basin. In: Geology and Mineral Resources of Western Australia, pp. 457–495. Geological Survey of Western Australia Memoir 3.
- HOCKING R M, MOORS H T & VAN DE GRAAFF J E 1987. Geology of the Carnarvon Basin, Western Australia. Geological Survey of Western Australia Bulletin 133.
- HOCKING R M, PLAYFORD P E, HAINES P.W. & MORY A J 2008. Paleozoic geology of the Canning Basin—a field guide Geological Survey of Western Australia Record 2008/18.
- HOLLAND T 2013. Pectoral girdle and fin anatomy of Gogonasus andrewsae Long 1985: implications for tetrapodomorph limb evolution. Journal of Morphology 274, 147–164.
- Holland T & Long J A 2009. On the phylogenetic position of *Gogonasus andrewsae* Long J. 1985, within the Tetrapodamorpha. *Acta Zeologica* 90, 285–96
- JARVIK E 1980. Basic structure and evolution of vertebrates. Academic Press, London.
- JOHANSON Z 2003. Placoderm branchial and hypobranchial muscles and origins in jawed vertebrates. *Journal of Vertebrate Paleontology* 23, 735–749.
- Johanson Z & Trinajstic K 2014. Fossilized ontogenies: the contribution of placoderm ontogeny to our understanding of the evolution of early gnathostomes. *Palaeontology* DOI: 10.1111/pala.12093.
- JONES P, METCALFE I, ENGEL B A, PLAYFORO G, RIGBY J, ROBERTS J, TURNER S & WEBB G E 2000. Carboniferous palaeobiogeography of Australasia. In: Wright A J, Young G C, Talent J A & Laurie J R (eds) Palaeobiogeography of Australasian faunas and floras, pp. 259–286. Memoir of the Association of Australasian Palaeontologists 23.
- Karpinsky A P 1899. On the edestid remains and its new genus *Helicoprion. Zapiski Imperatorski Akademii Nauk* 7, 1–67 (in Russian).
- KARPINSKY A P 1912. On Helicoprion and other Edestidae. Proceedings of the Russian Mineralogical Society 49, 69–94 (in Russian).
- KLAPPER G 1989. The Montagne Noire Frasnian (Upper Devonian) conodont succession. *In*: McMillan N J, Embry A F & Glass D J (eds) *Devonian of the World*, vol 3, pp. 449–468. Canadian Society of Petroleum Geologists Memoir 14.
- LONG J A 1985. A new osteolepidid fish from the Upper Devonian Gogo Formation, Western Australia. Records of the Western Australian Museum 12, 361–377.
- LONG J A 1986. A new Late Devonian acanthodian fish from Mt. Howitt, Victoria, Australia, with remarks on acanthodian biogeography. Proceedings of the Royal Society of Victoria 98, 1– 17.
- LONG J A 1987. A new dinichthyid fish (Placodermi: Arthrodira) from the Upper Devonian of Western Australia, with a discussion of dinichthyid interrelationships. Records of the Western Australian Mnseum 13, 515–540.
- Long J A 1988. Late Devonian fishes from Gogo, Western Australia National Geographic Research 4, 436–449.
- Long J A 1990. Late Devonian chondrichthyans and other microvertebrate remains from northern Thailand. *Journal of Vertebrate Palcontology* 10, 59–71.

- Long J A 1991. The long history of Australian fossil fishes. *In:* Vickers-Rich P, Monaghan J M, Baird R F & Rich T H (eds) *Vertebrate palaeontology of Australasia*, pp. 337–428. Pioneer Design Studio, Melbourne.
- Long J A 1993. Palaeozoic vertebrate biostratigraphy of South-East Asia and Japan. *In*: Long J A (ed.) *Palaeozoic vertebrate biostratigraphy and biogeography*, pp. 277–289. Belhaven Press, London.
- Long J 1995. *The rise of fishes*. The Johns Hopkins University Press, Baltimore.
- Long J A 2004. Gogo fish! The story of the Western Australian State Fossil emblem. Western Australian Museum, Perth.
- LONG J A 2006. Swimming in Stone: The Amazing Gogo Fossils of the Kimberley. Fremantle Press, Perth.
- Long J A & Trinajstic K 2000. Devonian microvertebrate faunas of Western Australia. In: Blieck A & Turner S (eds) Palaeozoic vertebrate biochronology and global marine/non-marine correlation. Final report of IGCP 328 (1991–1996), pp. 471–486. Courier Forschungsinstitut Senckenberg 223.
- LONG J A & TRINAISTIC K 2010. The Late Devonian Gogo Formation Lägerstatte of Western Australia: exceptional early vertebrate preservation and diversity. *Annual Review of Earth and Planetary Sciences* 38, 255–279.
- Long J A, Trinaistic K & Johanson Z 2009. Devonian arthrodire embryos and the origin of internal fertilization in vertebrates. *Nature* 457, 1124–1127.
- LONG J A, TRINAJSTIC K, YOUNG G C & SENOEN T 2008. Live birth in the Devonian period. *Nature* **453**, 650–652.
- LONG J A, YOUNG G C, HOLLANO T, SENDEN T & FITZGERALO E M G 2006. An exceptional Devonian fish sheds light on tetrapod evolution. Nature 444, 199–202.
- MACAOIE C I 2002. The lodont fish and conodonts from the Lower Devonian of Reefton, New Zealand. Alcheringa 26, 423–433.
- MAWSON R, TALENT J A, BEAR V C, BENSON D S, BROCK G A, FARRELL J R, HYLAND K A, PYEMONT B D, SLOAN T R, SORENTINO L, STEWART M I, TROTTER J A, WILSON G A & SIMPSON A G 1988. Conodont data in relation to resolution of Stage and zonal boundaries for the Devonian of Australia. *In:* McMillan N J, Embry A F & Glass D J (eds) *Devonian of the World*, vol 3, pp. 485–527. Canadian Society of Petroleum Geologists Memoir 14.
- McNamara K, Feist R & Ebach M 2009. Patterns of evolution and extinction in the last harpetid trilobites during the Late Devonian (Frasnian). *Palaeontology* **52**, 11–33.
- MELENDEZ I, GRICE K, TRINAJSTIC K, LADJAVARDI M, GREENWOOD P & THOMPSON K 2013. Biomarkers reveal the role of photic zone euxinia in exceptional fossil preservation: an organic geochemical perspective. Geology 41, 123–126.
- Miles R S 1967. Observations on the ptyctodont fish Rhamphodopsis Watson. Zoological Journal of the Linnean Society of London 47, 99–120.
- MILES R S 1969. Features of placoderm diversification and the evolution of the arthrodire feeding mechanism. *Transactions of the Royal Society of Edinburgh* 68, 123–170.
- MILES R S 1971. The Holonematidae (placoderm fishes): a review based on new specimens of *Holonema* from the Upper Devonian of Western Australia. *Philosophical Transactions of the Royal Society B* 263, 101–234.
- MILES R S & YOUNG G C 1977. Placoderm interrelationships reconsidered in the light of new ptyctodontids from Gogo Western Australia. Linnean Society of London Symposium Series 4, 123–198.
- Moors H T 1981. An alluvial fan-fluvial plain depositional model for the Devonian Willaraddie Formation and Manubia sandstone of the Carnarvon Basin, W.A. Geological Survey of Western Australia Annual Report for 1980, 62–67.
- NICOLL R S 1977. Conodont apparatuses in an Upper Devonian palaeoniscoid fish from the Canning Basin, Western Australia. BMR Journal of Australian Geology & Geophysics 2, 217–278.

- NICOLL R. 1979. A Late Devonian age for the Munabia Sandstone, Carnarvon Basin, W.A. Bureau of Mineral Resource, Professional Oil Geology 79/034 (unpubl.).
- ØRVIG T 1960. New finds of acanthodians, arthrodires, crossopterygians, ganoids and dipnoans in the upper Middle Devonian Calcareous Flags (Oberer Plattenkalk) of the bergisch-Paffrath Trough. (Part 1). Paläontologische Zeitschrift 34, 295-335.
- Patterson C 1965. The phylogeny of the chimaeroids. Philosophical Transactions of the Royal Society B 249, 101–219.
- Parkes R 1995. Late Silurian-Early Devonian vertebrate microremains from Nevada and southeastern Australia: biochronology, biogeography and application of novel histological techniques. BSc (Hons) thesis, Macquarie University, North Ryde (unpubl.).
- PLAYFORD P E, HOCKING R M & COCKBAIN A E 2009. Devonian reef complexes of the Canning Basin, Western Australia. Geological Survey of Western Australia Bulletin 145.
- Qu Q, Sanchez S, Blom H, Tafforeau P & Ahlberg P 2013a. Scales and tooth whorls of ancient fishes challenge distinction between external and oral 'teeth' *PloS One* 8 (8), e71890.
- Qu Q, Zhu M & Wang W 2013b. Scales and dermal skeletal histology of an early bony fish *Psarolepis romeri* and their bearing on the evolution of rhombic scales and hard tissues. *PLoS ONE* 8, e61485.
- RITCHIE A 1973. Wuttagoonaspis gen. nov., an unusual arthrodire from the Devonian of western New South Wales, Australia. Palacontographica A 143, 58–72.
- RITCHIE A 1975. Groenlandaspis in Antarctica, Australia and Europe. Nature 254, 569–574.
- RITCHIE A & GILBERT-TOMLINSON J 1977. First Ordovician vertebrates from the Southern Hemisphere *Atcheringa* 1, 351–368.
- ROELOFS B, TRINAJSTIC K, PLAYTON T E, TOHVER E, HAINES P, HOCKING R, BARHAM M, HANSMA J, HILLBUN K, GRICE K, MAODU Y, RATCLIFFE K, PISAREVSKY S & MONTGOMERY P 2013. Vertebrate biostratigraphy from the Devonian and Carboniferous in the Canning Basin, Western Australia. In: Keep M & Moss S J (eds) The Sedimentary Basins of Western Australia 4, Abstracts. Proceedings of the Petroleum Exploration Society of Australia Symposium, Perth, WA, 2013.
- Rücklin M, Donoghue P C J, Johanson Z, Trinajstic K, Marone F & Stampanoni M 2012. Development of teeth and jaws in the earliest jawed vertebrates. *Nature* 491, 748–751.
- Sanchez S, Ahlberg P E, Trinajstic K M, Mirone A & Tafforeau P 2012. Three-dimensional synchrotron virtual paleohistology: a new insight into the world of fossil bone microstructures. *Microscopy and Microanalysis* 18, 1095–1105.
- SANCHEZ S, DUPRET V, TAFFOREAU P, TRINAJSTIC K M, RYLL B, GOUTTENOIRE P-J, WRETMAN L, ZYLBERBERG L, PEYRIN F & AHLBERG P E 2013. 3D Microstructural architecture of muscle attachments in extant and fossil vertebrates revealed by Synchrotron Microtomography. PLos ONE 8, e56992.
- SANSOM I J, HAINES P W, ANDREEV P & NICOLL R S 2013. A new pteraspidomorph from the Nibil Formation (Katian, Late Ordovician) of the Canning Basin, Western Australia. *Journal* of Verlebrate Paleontology 33, 764–769.
- Sansom 1 J, Miller G C, Heward A, Davies N S, Booth G A, Fortey R A & Paris F 2009. Ordovician fish from the Arabian peninsular. *Palaeontology* 52, 337–342.
- SEDDON G 1969. Conodont and fish remains from the Gneudna Formation, Carnarvon Basin, Western Australia. *Journal of the Royal Society of Western Australia* 52, 21–30.
- SHEN J, WEBB G & JELL J 2008. Platform margins, reef facies, and microbial carbonates; a comparison of Devonian reef complexes in the Canning Basin, Western Australia, and the Guilin region, South China. *Earth-Science Reviews* 88, 33–59.
- SMITH M & JOHANSON Z 2003. Separate evolutionary origins of teeth from evidence in fossil jawed vertebrates. Science 299, 1235–1236.

- STRUCKMEYER H I M and TOTTERDELL J M (Editors) 1992. Australia, Evolution of a Continent / BMR Palaeogeographic Group. Australian Government Publishing Service, Canberra.
- Tapanila L, Prutit J, Pradel A, Wilga C, Ramsay J, Schlader R, Dider D. 2013. Jaws for a spiral tooth whorl: CT images reveal novel adaptation and phylogeny in fossil *Helicoption*. *Biology Letters* doi 10.1098/rsbl.2013.0057.
- THOMAS G A 1957. Lower Carboniferous deposits in the Fitzroy Basin, Western Australia. *Australian Journal of Science* 19, 160–161.
- Trinajstic K 1999a. New anatomical information on *Hotonema* (Placodermi) based on material from the Frasnian Gogo Formation and the Givetian–Frasnian Gneudna Formation, Western Australia. *Geodiversitas* 21, 69–84.
- Trinajstic K 1999b Scales of palaeoniscoid fishes (Osteichthyes: Actinopterygii) from the Late Devonian of Western Australia Records of the Western Australian Museum Supplement 57, 93–106.
- Trinajstic K 1999c. Scale morphology of the Late Devonian palaeoniscoid *Moythomasia durgaringa* Gardiner and Bartram, 1977. *Alcheringa* 23, 9–19.
- TRINAJSTIC K 2000. Conodonts, the lodonts and phoebodonts—together at last *Geological Society Of Australia Abstracts* 61, 121.
- Trinajstic K 2001a. A description of additional variation seen in the scale morphology of the Frasnian thelodont *Australotepis* seddoni Turner and Dring, 1981. Records of the Western Australian Museum Supplement 20, 237–246.
- TRINAJSTIC K 2001b. Acanthodian microremains from the Frasnian Gneudna Formation, Western Australia. Records of the Western Australian Muscum Supplement 20, 187–198.
- Trinajstic K, Boisvert C, Long J, Maksimenko A, Johanson Z in press a. Pelvic and reproductive structures in placoderms (stem gnathostomes). *Biological Reviews*
- TRINAJSTIC K & GEORGE A D 2009. Microvertebrate biostratigraphy of Upper Devonian (Frasnian) carbonate rocks in the Canning and Carnarvon basins of Western Australia. *Palaeontology* 52, 641.
- Trinajstic K, Grice K, Downes P, Böttcher M, Melendez J, Dellwig O, Burrow C & Verrall M in press b. Mineralized muscles and organs in a 380 million year old actinopterygian fish from the Gogo Formation, Western Australia. *PLoS ONE*.
- Trinajstic K & Johanson J 2014. Fossilized ontogenies: the contribution of placoderm ontogeny to our understanding of the evolution of early gnathostomes *Palaeontology* **57**, 505–516.
- Trinajstic K & Long J A 2009. A new genus and species of ptyctodont (Placodermi) from the Late Devonian Gneudna Formation, Western Australia, and an analysis of ptyctodont phylogeny. *Geological Magazinc* 146, 743–760.
- TRINAJSTIC K, LONG J, JOHANSON Z, YOUNG G & SENDEN T 2012. New morphological information on the ptyctodontid fishes (Placodermi, Ptyctodontida) from Western Australia. *Journal of Verlebrate Pateontology* 32, 757–780.
- Trinajstic K, Marshall C, Long J A, Bifield K 2007. Exceptional preservation of nerve and muscle tissues in Late Devonian placoderm fish and their evolutionary implications. *Biology Letters* 3, 197–200.
- Trinajstic K, Sanchez S, Dupret V, Tafforeau P, Long J, Young G, Senden T, Boisvert C, Power N & Ahlberg P E 2013. Fossil inusculature of the most primitive jawed vertebrates. *Science* 341, 160–164.
- TURNER S 1982a. Thelodonts and correlation. In: Rich P V & Thompson E M (eds) The Fossil Vertebrate Record of Australasia, pp. 128–132. Monash University Offset Printing Unit, Clayton.
- Turner S 1982b. Middle Palaeozoic elasmobranch remains from Australia. *Journal of Vcrtebrate Paleontology* 2, 117–131.
- Turner S 1990. Early Carboniferous shark remains from the Rockhampton District, Queensland. *Memoirs of the Queensland Museum* 28, 65–73.

- Turner S 1991. Palaeozoic vertebrate microfossils in Australasia. In: Vickers-Rich P, Monaghan J M, Baird R F & Rich T H (eds) Vertebrate palaeontology of Australasia, pp. 429–464. Pioneer Design Studio, Melbourne.
- Turner S 1993. Palaeozoic microvertebrate biostratigraphy of Eastern Gondwana. *In*: Long J A (ed.) *Palaeozoic vertebrate biostratigraphy and biogeography*, pp. 174–207. Belhaven Press, London.
- Turner S 1995. Defining Devonian and D/C microvertebrate faunal assemblages or zones for eastern Gondwana. *In*:
 Turner S (ed.) *Palaeozoic Microvertebrates* 1995 *Report: Moscow-94 Workshop*, pp. 43–52. Ichthyolith Issues Special Publication 1.
- Turner S 1997. Sequence of Devonian the Indon't scale assemblages in East Gondwana. In: Klapper G, Murphy M A & Talent J A (eds) Paleozoic sequence stratigraphy, biostratigraphy, and biogeography: studies in honor of J. Granville ("Jess") Johnson, pp. 295–315. Geological Society of America Special Publication 321.
- TURNER S 2009. Fossil Lagerstätten in Australia: discovery and politics. *Iu*: Pemberton G (ed.) *INHIGEO 34 Fossils & Fuels*, Abstracts, pp. 73–74. University of Calgary, August 10-14 2009.
- TURNER S 2014. Report on Silurian and Devonian microvertebrates from Western Australian boreholes. Report to Geological Survey of Western Australia (unpubl.).
- Turner S, Basden A & Burrow C J 2000. Devonian vertebrates of Queensland. In: Blieck A & Turner S (eds) Palaeozoic vertebrate biochronology and global marine/non-marine correlation. Final report of IGCP 328 (1991–1996), pp. 487–522. Courier Forschungsinstitut Senckenberg 223.
- TURNER S, BLIECK A R M & NOWLAN G S 2004. Cambrian—Ordovician vertebrates. In: Webby B D, Droser M, Feist R & Percival I (eds) IGCP410 The Great Ordovician Biodiversity Event, pp. 327–335. Columbia University Press, New York.
- Turner S, Burrow C J, Gholamalian H & Yazdi M 2002. Late Devonian (early Frasnian) microvertebrates and conodonts from the Chahriseh area near Esfahan, Iran. *Memoirs of the Association of Australasian Palacontologists* 27, 149–159.
- Turner S & Dring R S 1981. Late Devonian thelodonts (Agnatha) from the Gneudna Formation, Carnarvon Basin, Western Australia. *Alcheringa* 5, 39–48.
- Turner S, with contributions from Jones R, Leu M, Long J A, Palmieri V & Stewart 1 1994. IGCP 328: Carboniferous shark remains of Australia. In: Mawson R & Talent J A (eds) APC-94 (papers from the First Australian Palaeoutological Convention, Macquarie University, 7–9 February 1994, Abstracts, p. 58.
- Turner S, Trinajstic K, Hairapetian V, Janvier P & Macadie I 2004. Thelodonts from western Gondwana. In: Richter M & Smith M M (eds) 10th International Symposium on early vertebrates/lower vertebrates. Gramada, Brazil, 24–28 May 2004. Programme and Abstracts, pp. 45–46. UFRGS & Sociedade Brasiliera de Paleontologia.
- Turner S, Vergoossen J M J & Young G C 1995. Fish microfossils from Irian Jaya. Memoirs of the Australasian Association of Palaeontologists 18, 165–178.
- UPENIECE I 1996. Lodeacauthus gaugicus n. g. et sp. (Acanthodii: Mesacanthidae) from the Late Devonian of Latvia. Modern Geology 20, 383–398.
- Vergoossen J M J 1995. Remarks on microremains of acanthodians (Gnathostomata) from the late Pridoli of

- Manbrook (Upper Silurian, Great Britain). Geobios 28, 399-401.
- WANG S & TURNER S 1995. A reappraisal of Upper Devonian– Lower Carboniferous vertebrate microfossils in South China. Professional Papers of Stratigraphy and Palaeontology 26, 59–70.
- Watson D M S 1934. The interpretation of arthrodires, Proceedings of the Zoological Society of London 3, 437–464.
- WATSON D M S 1938. On Rhamphodopsis, a ptyctodont from the Middle Old Red Sandstone of Scotland. Transactions of the Royal Society of Edinburgh 59, 397–410.
- Young G C 1986. The relationships of placoderm fishes. Zoological Journal of the Linnean Society of London 88, 1–56.
- Young G C 1987. Devonian fish remains from Billiluna, eastern Canning Basin, Western Australia. BMR Journal of Australian Geology & Geophysics 10, 179–192.
- YOUNG G C 1991. The first armoured agnathan vertebrates from the Devonian of Australia. In: Chang M-M, Liu Y-H & Zhang G-R (eds) Early vertebrates and related problems of evolutionary biology, pp. 67–85. Science Press, Beijing.
- Young G C 1993. Middle Palaeozoic macrovertebrate biostratigraphy of Eastern Gondwana. In: Long J A (ed.) Palaeozoic vertebrate biostratigraphy and biogeography, pp. 208– 251. Belhaven Press, London.
- Young G C 1997. Ordovician microvertebrate remains from the Amadeus Basin, central Australia. *Journal of Vertebrate Paleontology* 17, 1–25.
- Young G C 2005. An articulated phyllolepid fish (Placodermi) from the Devonian of central Australia: implications for non-marine connections with the Old Red Sandstone continent. *Geological Magazine* 142, 173–186.
- Young G C 2009. New arthrodires (Family Williamsaspididae) from Wee Jasper, New South Wales (Early Devonian), with comments on placoderm morphology and palaeoecology. Acta Zoologica 90, 69–82
- Young G C, Burrow C J, Long J A, Turner S & Choo B 2010. Devonian macrovertebrate assemblages and biogeography of East Gondwana (Australasia, Antarctica). *Palaeoworld* 19, 55–74.
- Young G C & Goujet D 2003. Devonian fish remains from the Dulcie Sandstone and Cravens Peak Beds, Georgina Basin, central Australia. Records of the Western Australian Museum Supplement 65, 1–85.
- Young G C, Karatajute-Talimaa V & Smith M M 1996. A possible Late Cambrian vertebrate from Australia. *Nature* 383, 810–812.
- Young G C & Turner S 2000. Devonian microvertebrates and marine nonmarine correlation in East Gondwana: overview. 111: Blieck A & Turner S (eds) Palaeozoic vertebrate biochronology and global marinehon-marine correlation. Final report of IGCP 328 (1991–1996), pp. 453–470. Courier Forschungsinstitut Senckenberg 223.
- Young G C, Turner S, Owen M, NICOLL R S, LAURIE J R & GORTER J D 1987. A new Devonian fish fauna, and revision of post-Ordovician stratigraphy in the Ross River Syncline, Amadeus Basin, central Australia. BMR Journal of Australian Geology & Geophysics 10, 233–242.
- ZHU M, YU X B, AHLBERG P E, CHOO B, LU J, QIAO T, ZHAO W, JIA L, Błom H & ZHU Y A 2013. Silurian placoderm with osteichthyan-like marginal jaw bones. *Nature* **502**, 188-193.

Received 22 February 2014; accepted 1 June 2014



Devonian Great Barrier Reef of the Canning Basin, Western Australia: the evolution of our understanding

P E PLAYFORD*, R M HOCKING & A E COCKBAIN†

Geological Survey of Western Australia, 100 Plain Street, East Perth, WA 6004, Australia.

Devonian reef complexes are spectacularly exposed along the northern margin of the Canning Basin in Western Australia, and have become renowned as 'The Devonian Great Barrier Reef'. The geological literature on these rocks dates back to 1884 and the first studies of the biostratigraphy were conducted during the 1940s. Geologists of the Commonwealth Bureau of Mineral Resources were the first to systematically map the Devonian rocks, during the late 1940s and early 1950s, and since then studies by many individuals and organisations have progressively increased knowledge of the stratigraphy and paleontology of these reef complexes. The Geological Survey of Western Australia's research culminated in 2009 with the publication of a comprehensive bulletin on the geology of the reef complexes.

KEYWORDS: allochthonous block, atoll, barrier reef, bioherm, Canning Basin, cyclicity, depositional dip, Devonian, facies, mass extinction, mineralisation, paleontology, pinnacle reef, reef complexes, sequence stratigraphy, stromatolite, stylolitisation.

INTRODUCTION

Middle and Upper Devonian reef complexes form a series of spectacular limestone ranges that extend for some 350 km along the northern margin of the Canning Basin (Figures 1, 2). They are acknowledged to constitute the best example in the world of an ancient barrier reef system, and have become widely known as 'The Devonian Great Barrier Reef'.

Publications and unpublished reports considered to be turning points in the understanding of these reef complexes are summarised below. There are many more publications than those referenced here — for a comprehensive bibliography readers can refer to Playford *et al.* (2009).

FIRST DISCOVERY

The first geologist to examine these rocks was the Government Geologist E T Hardman, as a member of John Forrest's expedition exploring the area in 1883 (Hardman 1884). He examined the Napier Range at Windjana Gorge ('Devil's Pass': Figure 3), Geikie Gorge, Mt Pierre and adjoining areas (Playford & Ruddock 1985). Hardman did not recognise these rocks as reef deposits, and concluded that they were Carboniferous in age. However, examination of his fossil collections soon showed them to be Devonian (Nicholson 1890; Hinde 1890; Foord 1890).

RECOGNITION OF REEFS

Arthur Wade, while working for the Freney Kimberley Oil Company, was the first geologist to recognise that these limestones constitute reef deposits (Wade 1924),

and he later described them as being remnants of an 'ancient barrier reef' (Wade 1936).

PIONEERING PALEONTOLOGY AND BIOSTRATIGRAPHY

Curt Teichert, then with the University of Western Australia, worked on the Devonian reefs in association with geologists of Caltex (Australia) Oil Development Pty Ltd, who were assessing the oil prospects of the Canning Basin. Teichert examined the Devonian paleontology and biostratigraphy, publishing a series of papers on what he termed the 'Great Devonian Barrier Reef' (Teichert 1939, 1941, 1943, 1947, 1949). He was the first to recognise the facies equivalence of various parts of the complexes and their associated conglomerates (Figure 4: Teichert 1949). Although he was able to spend relatively little time in the field, Teichert laid firm foundations for subsequent studies of the reef complexes. Indeed, he was ahead of his time — he understood these rocks better than some geologists who studied them subsequently.

MAPPING BY THE COMMONWEALTH BUREAU OF MINERAL RESOURCES

From 1948 to 1952 the Commonwealth Bureau of Mineral Resources (BMR, now Geoscience Australia) mapped the full extent of the Devonian reef complexes for the first time, as part of a regional geological survey of the northern Canning Basin (then known as the 'Fitzroy Basin'). In 1953 the manuscript of a bulletin on the geology of this area was destroyed in a fire at the Bureau's offices in Canberra, but it was subsequently rewritten by the same authors, all but one of whom were by then employed by WAPET (West Australian Petroleum Pty Ltd). Guppy et al. (1958) defined many rock units in the reef complexes, and realised that the

© Crown Copyright

^{*}Corresponding author 🖾 phil.playford@dmp.wa.gov.au

[†] Present address: 104 Hensman Street, South Perth, WA 6151, Australia.

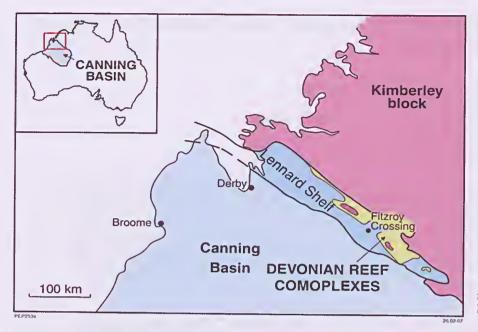


Figure 1 Locality map, Devonian reef complexes of the Canning Basin.

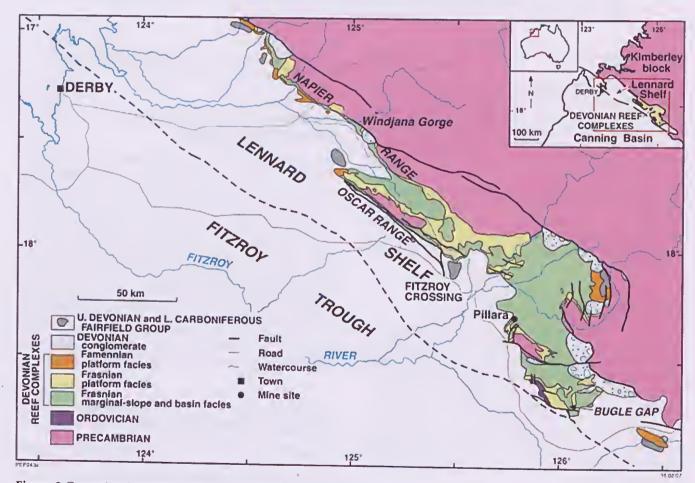


Figure 2 Generalised geological map, Devonian reef complexes of the Canning Basin.

steep dips in some of the limestones were largely depositional, but they did not recognise the equivalence of the various facies. They mistakenly concluded that the Pillara Limestone is entirely Middle Devonian (Givetian) in age and that it is overlain unconformably by Upper Devonian strata (Figure 5).

OSCAR RANGE STUDY

WAPET recognised that if these Devonian reef complexes extend into the subsurface, they would have a high potential for petroleum, because similar Devonian reefs in Alberta were known to contain large oil reserves. The



n by H. C. Prinsep, from a sketch by E. T. Hardman.

THE DEVIL'S PASS.

ON THE LENNARD RIVER.

Figure 3 Sketch by E T Hardman of the southern entrance to Windjana Gorge ('Devil's Pass').

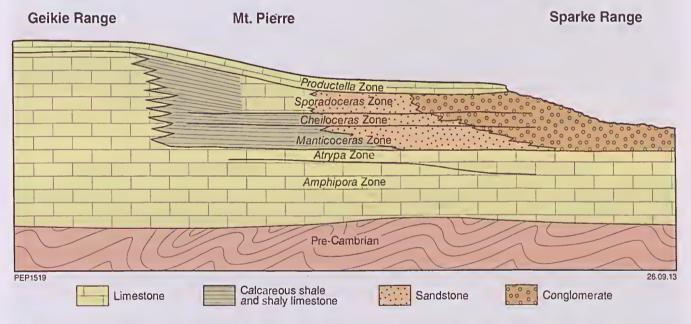
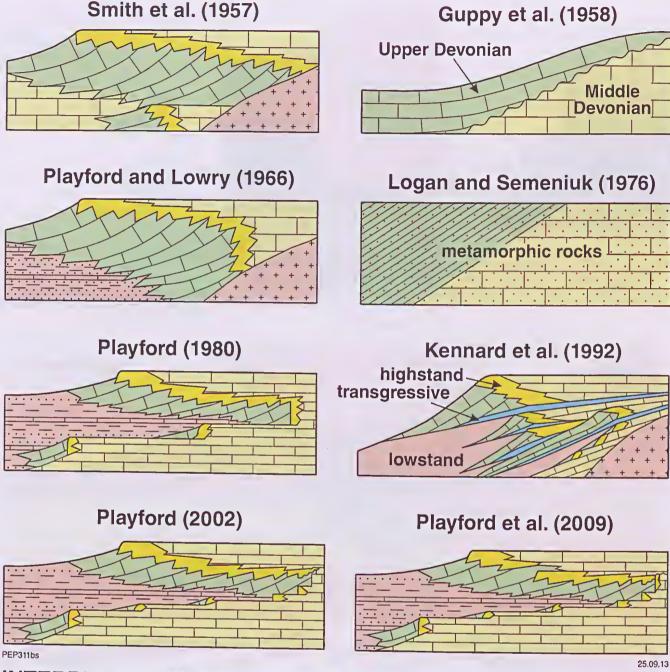


Figure 4 Diagrammatic cross-section illustrating the facies and paleontological zones of Devonian reef complexes between Geikie Range and Sparke Range, as interpreted by Teichert (1949 plate 6).

company concluded that there was a need for a better understanding of these reef complexes, and consequently a detailed study of the Oscar Range reef complex was undertaken in 1956 (Smith *et al.* 1957).

In this study Smith and Williams were responsible for the mapping, while Playford made periodic visits to the field and studied the petrology of the rocks, while becoming familiar with the literature on ancient reef complexes. One of the publications that he studied was that of King (1942) on the Permian reef complex of West Texas and southeastern New Mexico, in which he showed that distinct facies could be recognised in the reef complex. Playford concluded that comparable facies might be present in the Oscar Range reef complex, and as a result that was proved to be the case: three basic facies — reef, back reef, and fore reef — were recognised there (Smith *et al.* 1957) (Figure 5). It was also confirmed that the steep dips in fore-reef deposits are largely depositional.

Another important outcome of this work was recognition of the major role played by microbes in constructing the reefs. Those microbes, first seen in thinsections, were termed 'ghost algae', and were later recognised as the microbe *Renalcis* (Playford & Lowry 1966; Wray 1967; Playford 1967). That microbe would later be found to also occur in the Canadian reef complexes.



INTERPRETIVE MODELS OF THE REEF COMPLEXES 1957-2009

Figure 5 Diagram illustrating some changing concepts since 1957 in interpretation of the Devonian reef complexes.

WINDJANA GORGE

A study of the Upper Devonian reef complex at Windjana Gorge in the Napier Range was undertaken for WAPET in 1958 (Playford & Johnstone 1959; Playford 1961) (Figure 6). A notable outcome of that work was recognition of the spectacular exposure in the gorge that would later become known as 'The Classic Face' (Figure 7).

MAPPING AND ASSOCIATED RESEARCH BY THE GEOLOGICAL SURVEY OF WESTERN AUSTRALIA

Systematic mapping and interpretation of the reef complexes was conducted during 1962 and 1963 for the Geological Survey of Western Australia (GSWA), the results being published in Bulletin 118 (Playford & Lowry 1966). Among the outcomes of that study were recognition



Figure 6 Aerial view of the Napier Range at Windjana Gorge looking northwest. The sinuous front of the range is essentially the late Famennian reef scarp.



Figure 7 Panoramic view of the Classic Face at Windjana Gorge, showing flat-bedded back-reef and reef-flat limestones on the right, passing into massive reef-margin in the centre and steeply dipping marginal-slope deposits on the left.

of atolls and pinnacle reefs in the eastern part of the outcrop area (Figures 8, 9) and of the importance of contemporary tectonism in controlling development of the reef complexes. Fracturing of early-cemented limestones, resulting from that tectonism, formed networks of neptunian dykes (Figure 10) and gave rise to megabreccia

debris flows and isolated allochthonous blocks on marginal slopes in front of the reefal platforms (Figures 11, 12). Large masses of reef limestone in fore-reef deposits, previously considered to be bioherms, were now recognised as allochthonous reef blocks, in some cases capped by deep-water microbial limestone (Figure 12).



Figure 8 Aerial view looking north over the Laidlaw Range reef complex, showing (1) the Laidlaw Range atoll; (2) the 'tail' of Glenister Knolls patch reefs; (3) Ross Hill (Lower Permian sandstone); (4) Smith Knoll pinnacle reef; (5) Lloyd Hill atoll; and (6) Wade Knoll pinnacle reef.



Figure 9 Aerial view of Wade Knoll pinnacle reef looking south, showing concentric marginal-slope deposits and cyclic basin strata surrounding the reef pinnacle.



Figure 10 Aerial view looking east over the northeast side of the Oscar Range. Morown Cliff, at the front of the range, is essentially the exhumed late Famennian reef scarp. Note linear corridors following neptunian dykes, parallel to the reef front, with a subsidiary fracture system at right angles to those dykes.

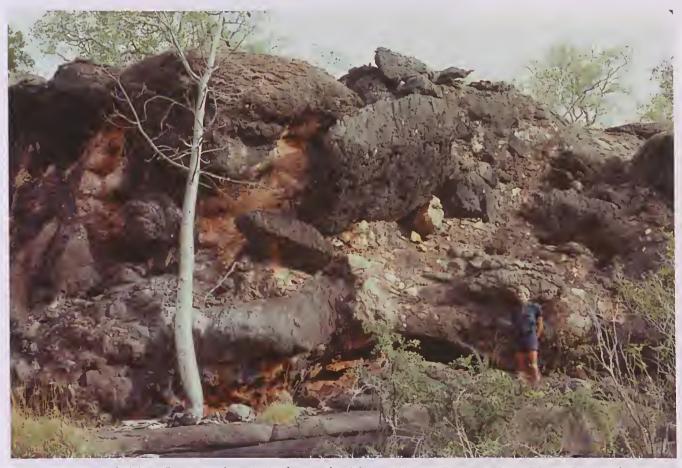


Figure 11 Typical debris-flow megabreccia in fore-reef subfacies (Napier Formation), at Dingo Gap in the Napier Range. The megabreccia is composed of blocks of reef and reefal-slope limestones in a matrix of calcarcous sandstone.



Figure 12 Allochthonous block of reef limestone in fore-reef subfacies (Napier Formation) 0.5 km south of McSherrys Gap, Napier Range. A thin (~15 cm thick) layer of deep-water stromatolites, at the foot of the person in the photograph, grew on top of the block after it came to rest.



Figure 13 Oncolites and capped oncolites in Sadler Limestone in the karst corridor on the west side of McWhae Ridge. The oncolites were built by *Girvanella*, and caps on the oncolites in the last layer were built by *Sphaerocodium*.



Figure 14 Receptaculitid in marginal-slope Sadler Limestone in the karst corridor on the west flank of McWhae Ridge, showing a geopetal infilling that marks the approximate horizontal at the time of deposition, compared with the depositional dip of the overlying marginal-slope limestones.



Figure 15 Early Famennian columnar stromatolites that grew vertically on a marginal slope in the Virgin Hills Formation at Ngumban Cliff.

BUGLE GAP AND DEEP-WATER STROMATOLITES

The GSWA, in association with the BMR, conducted detailed studies of reef complexes in the Bugle Gap area during 1968. One outcome of that work was the use of geopetal structures to quantify depositional dips and deduce paleobathymetry (Figures 13–15). It was shown that some stromatolites must have grown on marginal slopes in water depths of at least 35 m, and probably more than 100 m (Playford & Cockbain 1969). That conclusion was contrary to the belief, commonly held at that time, that stromatolites are solely intertidal phenomena (Logan 1961).

RECOGNITION OF CYCLICITY

Reid (1973a, b) was the first to recognise cyclicity in backreef limestones. The shallowing-upward cycles in that facies are deduced to be eustatic in origin, and are known as Milankovitch cycles (Figure 16). Subsequently it was shown that cyclicity can also be recognised in other facies of the reef complexes (Playford *et al.* 2009).

DEEP-WATER BIOHERMS

Playford *et al.* (1976) described the presence in the northeastern Oscar Range of major Late Devonian deepwater microbial and receptaculitid bioherms (Figure 17).



Figure 16 Low-level aerial view looking north, immediately north the eastern part of Windjana Gorge, showing strong cyclicity in Pillara Limestone, back-reef subfacies. Prominent white limestone is at the base of each cycle and is overlain by recessive-weathering calcareous sandstone.



Figure 17 Aerial view looking north over the southwest culmination of Elimberrie no. 2 bioherm. The width of the field of view in the centre of the photo is about 150 m.

ORIGINAL MORPHOLOGY

strong early cementation porosity destroyed little or no early cementation porosity retained REEFAL-SLOPE SUBFACIES FORE-REEF SUBFACIES REEF-MARGIN AND REEF-FLAT SUBFACIES BACK-REEF SUBFACIES SUBFACIES

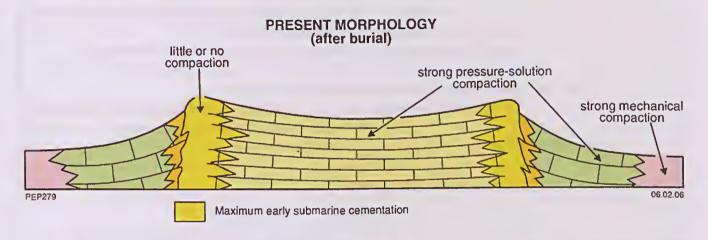


Figure 18 Diagram to illustrate changes in the morphology of the Devonian limestone platforms, resulting from pressure-solution compaction after burial.

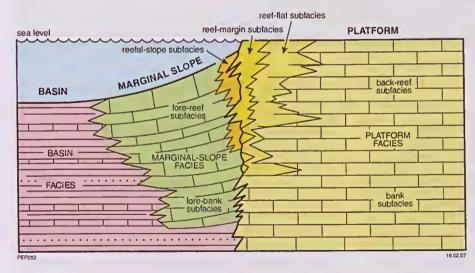


Figure 19 Diagrammatic crosssection illustrating the morphology and facies relationships of the reef complexes.

These remarkable bioherms grew over drowned Late Devonian pinnacle reefs, and are thought to be unique in the world.

'DYNAMIC METAMORPHISM'

A special publication of the Geological Society of Australia described the Devonian limestones as being products of dynamic metamorphism (Logan & Semeniuk 1976) (Figure 5). Those authors asserted that the limestones do not form reef complexes, but are instead the products of dynamic metamorphism, associated with intensive shear faulting, and with metamorphic grades as high as greenschist facies. Similar claims were put forward by Logan (1984) and Logan *et al.* (1994). However, those conclusions were not accepted by other authors, all of whom have recognised that the limestones represent unmetamorphosed reef complexes, and the supposed shear faults do not exist.

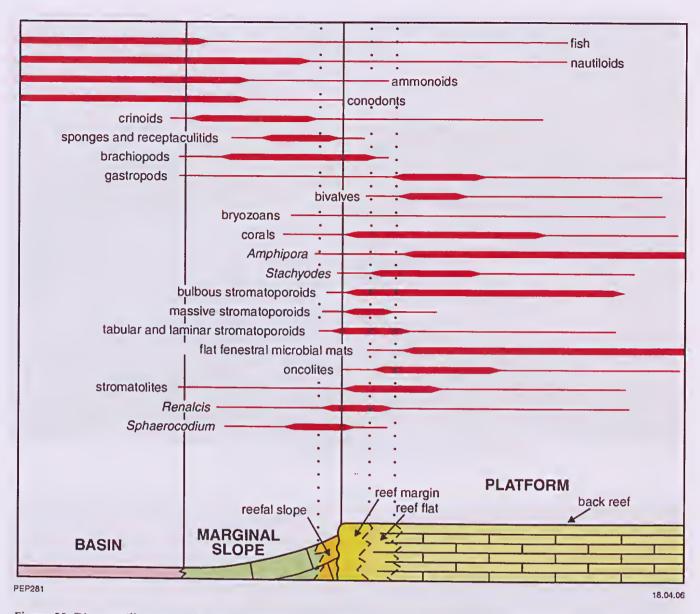


Figure 20 Diagram illustrating the biotic distribution of principal organisms in the Frasnian reef complexes.

GIVETIAN-FRASNIAN RETREATING AND BACKSTEPPING PLATFORMS, FAMENNIAN ADVANCING PLATFORMS, AND DIFFERENTIAL STYLOLITISATION

Playford (1980) published a paper entitled 'Devonian Great Barrier Reef of the Canning Basin, Western Australia', following a tour of the United States and Canada in 1978 as a Distinguished Lecturer of the American Association of Petroleum Geologists. A feature of that paper was the recognition of Givetian-Frasnian retreating and backstepping reefal platforms, followed during the Famennian by advancing platforms (Figure 5). It was also shown that differential compaction of the limestones has been controlled by variations in the degree of pressure-solution stylolitisation. Strong stylolitisation, and resulting compaction, has occurred in the back-reef subfacies, with little or no stylolitisation or compaction in reef-margin and reef-flat subfacies. This differential compaction has resulted in the characteristic 'dished' shape of many platforms (Figure 18).

FACIES NOMENCLATURE AND THE FRASNIAN/FAMENNIANMASS EXTINCTION

In a publication for a PESA (Petroleum Exploration Society of Australia) Canning Basin Symposium, Playford (1984) presented an updated facies nomenclature for the reef complexes (Figure 19), and also discussed the mass extinction at the Frasnian/Famennian (F/F) boundary (Figures 20–23). That mass extinction resulted in the loss of many marine species, so that the reef-building stromatoporoids, corals and microbes of the Frasnian were replaced by microbes, almost alone, during the Famennian. Marked changes also occurred in conodont and ammonoid faunas in basin and marginal-slope deposits at that boundary. The F/F boundary was shown to be unconformable in reef, reefal-slope, and back-reef facies, and conformable in basin facies and deeper fore-reef facies (Figures 22, 23).

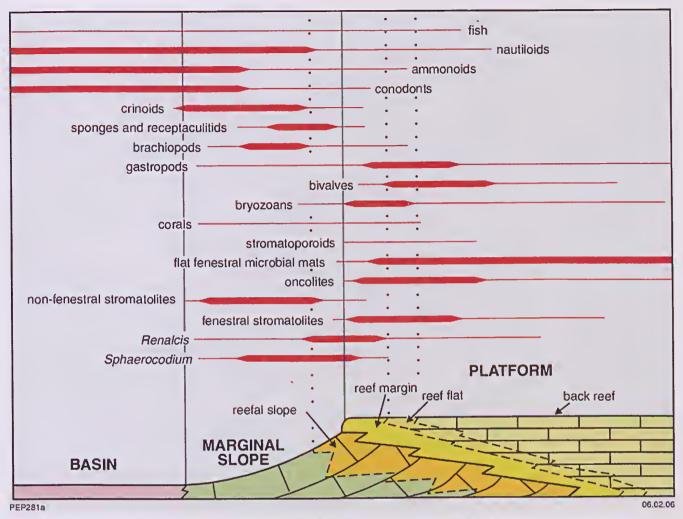


Figure 21 Diagram illustrating the biotic distribution of the principal organisms in the Famennian reef complexes.

PETROGRAPHY OF THE REEF COMPLEXES

Kerans (1985) made the first detailed studies of the petrology of the reef complexes, emphasising the importance of marine cementation in early diagenesis, and confirming earlier observations of Playford (1980, 1984). The strongest early cementation, with concomitant destruction of porosity, occurred in reef-margin, reef-flat, and reefal-slope deposits (Figures 24–26).

SEQUENCE STRATIGRAPHY

Kennard et al. (1992) were the first to apply the concept of sequence stratigraphy to the reef complexes. They adopted what has become known as the 'Exxon paradigm', whereby eustatic fluctuations in sea level are said to drive reciprocal sedimentation of highstand, transgressive and lowstand system tracts. They claimed that this gave rise to deposition of terrigenous conglomerates as lowstand deposits, and reefal platforms as highstand deposits, with thin intervening transgressive deposits (Figure 5). However, field studies by Playford et al. (2009) showed that most conglomerates in the area are highstand deposits that interfinger with platform, marginal-slope, and basin facies.

DEEP-WATER STROMATOLITE MOUNDS AND SULFIDE MINERALISATION

Deep-water stromatolite mounds, associated with barite mineralisation, and cut by iron-sulfide veins, were formed as exhalative deposits over cool-water seepages on the basin floors (Playford & Wallace 2001) (Figure 27). These deposits resulted from compaction-driven fluids, expelled from anoxic muds of the basin facies. In addition to nourishing stromatolites, the fluids gave rise to the associated barite and sulfide mineralisation (Figure 27). It had previously been known that a wide variety of other stromatolites grew on shallow reefal platforms and adjoining marginal slopes in the reef complexes, where they were associated with open-marine benthic faunas, whereas the exhalative stromatolites grew on and below the muddy floors of deep-water basins, without any associated benthic faunas (Figure 28).

EFFECTS OF THE PERMIAN GLACIATION

In a West Australian Basins Symposium (WABS), Playford (2002) discussed the role of the Permian glaciation in planing down the reef complexes below thick ice caps that flowed from south to north (Figure 29). Subglacial water below those ice caps resulted in



Figure 22 The Frasnian–Famennian unconformity near Limestone Spring in the northwestern Napier Range, showing well-bedded Nullara Limestone (Famennian back-reef subfacies) unconformably overlying crudely bedded Napier Formation (late Frasnian reefal-slope subfacies). The dip in the Napier Formation is largely depositional.

extensive networks of Nye channels and sub-glacial karst (Figures 30, 31).

PALEONTOLOGY

The Devonian paleontology of the Canning Basin is renowned worldwide, and a review of work on the various groups is beyond the scope of this paper. The most recent publications on important groups have been by Wray (1967) on microbes; Cockbain (1984) on stromatoporoids; Won (1997) on radiolarians; Jell & Jell (1999) on echinoderms; Klapper (2009) on conodonts; Becker & House (2009) on ammonoids; G. Playford (2009) on palynomorphs; Long & Trinajstic (2010) on fish; and Feist & McNamara (2013) on trilobites.

SYNTHESIS OF MORE THAN 50 YEARS OF RESEARCH

A detailed synthesis of more than 50 years of research on the Devonian Great Barrier reef by GSWA and its many collaborators was published by Playford *et al.* (2009) as Bulletin 145 of the Geological Survey. This major publication was based largely on remapping and detailed stratigraphic studies of the reef complexes, with associated paleontological research. It refines earlier understandings of the facies and stratigraphy, and presents an event-based sequence stratigraphy of the reef complexes. Siliciclastic conglomerates were shown to be tectonically driven and synchronous with the reef complexes, and tectonic versus eustatic controls on the cyclicity and development of the various facies were discussed.

The bulletin includes a guide to the most significant field localities and includes more than 530 colour photos and diagrams. The diagrams include a model illustrating the various facies recognised in the reef complexes (Figure 32), and another showing the lithostratigraphy, sequence stratigraphy and events responsible for backstepping and partial drowning of reefal platforms (Figure 33).

Accompanying the bulletin are a series of maps at scales of 1:500 000, 1:250 000, and 1:100 000 of the entire reef belt, and 1:50 000 and 1:25 000 of key areas. Also included are appendices on important elements of the

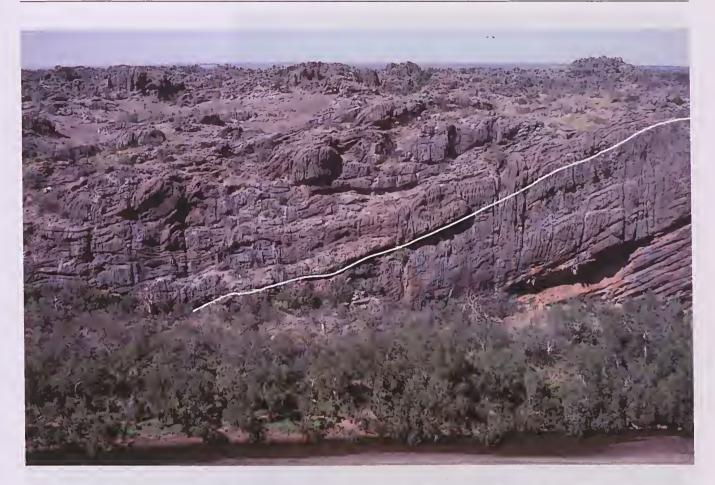
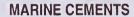


Figure 23 The Frasnian–Famennian boundary, marked by a white line, in marginal-slope deposits (Napier Formation) in the eastern part of Windjana Gorge, on its south side. The Frasnian deposits on the right are generally well bedded, whereas the Famennian deposits on the left are poorly bedded and marked by many allochthonous blocks of reef limestone. Note the undulating bedding, probably stromatolitic, above the boundary.



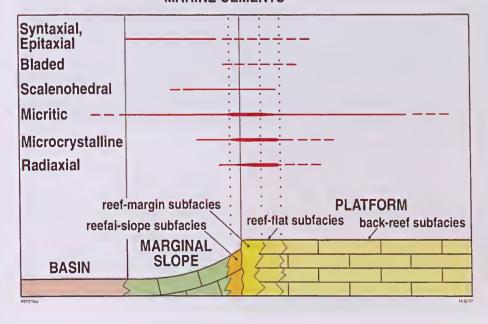


Figure 24 Diagram illustrating the distribution of various types of early marine cements in the reef complexes.



Figure 25 Thin-section of microbial stromatoporoid reef limestone (Pillara Limestone) showing a former large cavity, now filled with interlaminated fibrous sparry calcite and red cavity peloids, from an allochthonous block at McIntyre Knolls

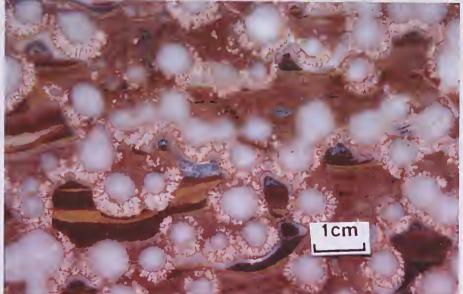


Figure 26 Polished slab of reef limestone (Pillara Limestone) from an allochthonous block in marginal-slope deposits at McIntyre Knolls, showing a colony of *Stachyodes* that fell over before being encrusted by *Renalcis*. The rest of the cavity system was then filled successively with red laminated peloidal limestone and clear sparry calcite.

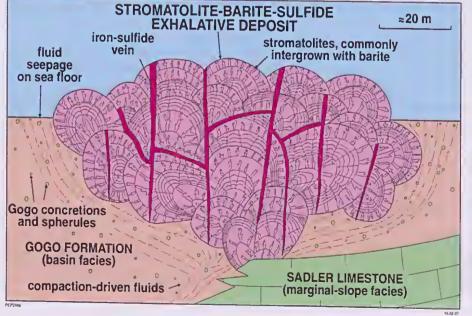


Figure 27 Diagrammatic crosssection through a Frasnian exhalative deposit, showing bulbous stromatolites, intergrown with barite and cut by iron-sulfide veins. The deposit was generated in deep water by compaction-driven fluids above the contact between Gogo Formation (basin facies) and Sadler Limestone (marginal-slope facies).

		PLAN SECTION		PLAN SECTION
COLUMNAR	Spaced ~0.5 m	0000	Scalloped ~0.25 m	
	Contiguous		Reticulate _~0.5 m	
	Branching ~0.25 m	· 0000	Undulous	
	Longitudinal	M Aaa	Domal1 m	
	Antiformal ~2 m		Exhalative ~5 m	

Figure 28 Diagram illustrating the different types of stromatolites recognised in the reef complexes.



Figure 29 Striated and polished glacial pavement in reef limestone exposed in the Goongewa box-cut, showing small-scale crag-and-tail structures. Ice movement was from right to left on the photo (south to north).

fossil biota (Klapper 2009; Becker & House 2009; G Playford 2009).

CONCLUSION

A great deal of research has been documented on this Devonian Great Barrier Reef since the first of Teichert's papers was published in 1939, but the potential remains for more research on various aspects of these remarkable reef complexes. One of the most pressing needs is to devise the means to achieve precise correlation between back-reef, reef, and marginal-slope deposits, and collaborative work, by several research workers, is now seeking to resolve that issue.



Figure 30 Aerial view of Kimberley Rover solution doline in the northern Laidlaw Range, looking northwest, showing outcrops of Lower Permian silicified sandstone within the doline, surrounded by karstified Pillara Limestone. Karst corridors follow joints in the limestone, and a large cave system (Kimberley Rover Cave) underlies the dark rugged limestone on the upper right.



Figure 31 Menyous Gap in the Pillara Range from the air, looking north. This gap, 2 km long, is interpreted to be a large subglacial channel, exhumed through the removal of Lower Permian deposits by Cenozoic erosion.

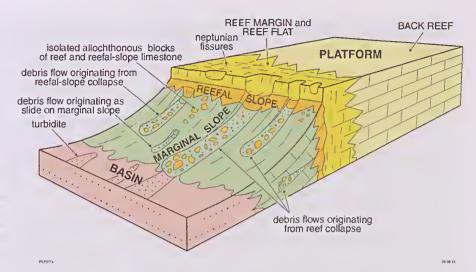


Figure 32 Block diagram illustrating the morphology of the reef complexes and relationships between platform, marginal-slope and basin facies, and associated features.

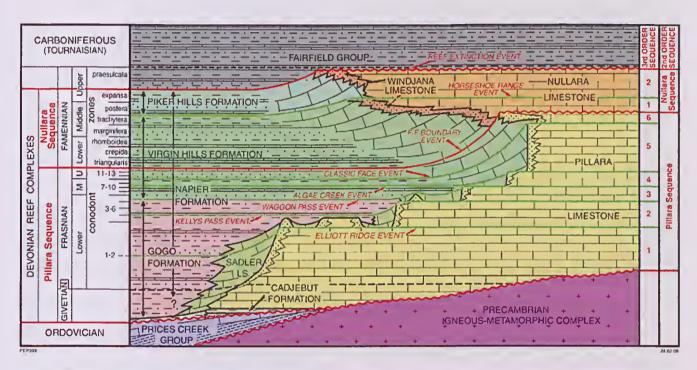


Figure 33 Diagrammatic section illustrating the lithostratigraphy, sequence stratigraphy and conodont biostratigraphy of Devonian reef complexes on the Lennard Shelf.

ACKNOWLEDGEMENT

This summary account of the reef complexes uses many illustrations from Playford *et al.* (2009), with minor changes. It is published with the permission of the Director, Geological Survey of Western Australia.

REFERENCES

BECKER T R & House M R 2009. Appendix 2, Devonian ammonoid biostratigraphy of the Canning Basin. *Geological Survey of Western Australia Bulletin* 145, 415–439.

COCKBAIN A E 1984. Stromatoporoids from the Devonian reef complexes, Canning Basin, Western Australia. Geological Survey of Western Australia Bulletin 129. Feist R & McNamara K J 2013. Patterns of evolution and extinction in proetid trilobites during the Late Devonian mass extinction event, Canning Basin, Western Australia. *Palacontology* 56, 229–259.

FOORD A H 1890. Description of fossils from the Kimberley District, Western Australia. *Geological Magazine* Dec. 3, v. 7, 98–106, 145–155.

Guppy D J, Lindner A W, Rattigan J H & Casey J N 1958. The geology of the Fitzroy Basin, Western Australia. *Bureau of Mineral Resources Bulletin* 36.

HARDMAN E T 1884. Report on the geology of the Kimberley District, Western Australia. Western Australian Parliamentary Papers, no. 31 of 1884; Government Printer, Perth.

HINDE G J 1890. Notes on the palaeontology of Western Australia, corals and Polyzoa. Geological Magazine Dec. 3, v. 7, 194–204.

- JELL P A & JELL J S 1999. Crinoids, a blastoid, and a cyclocystoid from the Upper Devonian reef complexes of the Canning Basin, Western Australia. Memoirs of the Queensland Museum 43, 201–236.
- Kennard J M, Southgate P N, Jackson M J, O'Brien P E, Christie-Blick N, Holmes A E & Sarg J F 1992. New sequence perspective on the Devonian reef complex and the Frasnian–Famennian boundary, Canning Basin, Australia. *Geology* 20, 1135–1138.
- Kerans C 1985. Petrology of Devonian and Carboniferous carbonates of the Canning and Bonaparte Basins, Western Australia. Western Australian Mining and Petroleum Research Institute Report 12.
- King P B 1942. Permian of west Texas and southeastern New Mexico. AAPG Bulletin 26, 535–753.
- KLAPPER G 2009. Appendix 1, Upper Devonian conodonts in the Canning Basin. Geological Survey of Western Australia Bulletin 145, 405–413.
- LOGAN B W 1961. Cryptozoon and associate stromatolites from the Recent, Shark Bay, Western Australia. Journal of Geology 69, 517–533.
- Logan B W 1984. Pressure responses (deformation) in carbonate sediments and rocks, analysis and application, Canning Basin. *In:* Purcell P G (ed.) *The Canning Basin, Western Australia*, pp. 235–251. Geological Society of Australia and Petroleum Exploration Society of Australia, Canning Basin Symposium, Perth.
- Logan B W, Frances D J & Economo M 1994. A carbonate dilaform, Brooking Springs, Canning Basin, W.A. *In*: Purcell P G & Purcell R R (eds) *The sedimentary basins of Western Australia*, pp. 703–726. Geological Society of Australia and Petroleum Exploration Society of Australia, West Australian Basins Symposium, Perth.
- LOGAN B W & SEMENIUK V 1976. Dynamic metamorphism, processes and products in Devonian carbonate rocks, Canning Basin, Western Australia. Geological Society of Australia Special Publication 6.
- LONG J A & TRINAJSTIC K 2010. The Late Devonian Gogo Formation Lagerstatte — exceptional preservation and diversity in early vertebrates. Annual Reviews of Earth and Planetary Sciences 38, 665–680.
- Niciolson H A 1890. Notes on the palacontology of Western Australia, Stromatoporoidea. *Geological Magazine* Dec. 3 v. 7, 193.
- Playford G 2009. Appendix 3, Review of Devonian palynology, Canning Basin. *Geological Survey of Western Australia Bulletin* 145, 441–444.
- PLAYFORD P E 1961. Upper Devonian reef complex at Windjana Gorge, Canning Basin, Western Australia. Geological Society of America Special Papers 68, 247–248.
- Playford P E 1967. Devonian reef complexes in the northern Canning Basin, Western Australia. In: Oswald D H (ed.) International Symposium on the Devonian System, Vol. 2, pp. 351–364. Alberta Society of Petroleum Geologists, Calgary.
- PLAYFORD P E 1980. Devonian 'Great Barrier Reef' of Canning Basin, Western Australia. AAPG Bulletin 64, 814–840.
- PLAYFORD P E 1984. Platform-margin and marginal-slope relationships in Devonian reef complexes of the Canning Basin. *In:* Purcell P G (ed.) *The Canning Basin, Western Australia*, pp. 189–234. Geological Society of Australia and Petroleum Exploration Society of Australia, Canning Basin Symposium, Perth.
- PLAYFORD P E 2002. Paleokarst, pseudokarst, and sequence stratigraphy in Devonian reef complexes of the Canning

- Basin, Western Australia. *Iu*: Keep M & Moss S J (eds) *The sedimentary basins of Western Australia* 3, pp. 763–793. Proceedings of the Petroleum Exploration Society of Australia Symposium, Perth.
- PLAYFORD P E & COCKBAIN A E 1969. Algal stromatolites: deepwater forms in the Devonian of Western Australia. *Science* 165, 1008–1010.
- PLAYFORD P E, COCKBAIN A E, DRUCE E C & WRAY J L 1976. Devonian stromatolites from the Canning Basin, Western Australia: *In:* Walter M R (ed.) *Stromatolites*, pp. 543–564. Elsevier, Amsterdam.
- PLAYFORD P E, HOCKING R M & COCKBAIN A E 2009. Devonian reef complexes of the Canning Basin, Western Australia. Geological Survey of Western Australia Bulletin 145.
- PLAYFORD P E & JOHNSTONE M H 1959. Upper Devonian reef complex at Windjana Gorge, Kimberley District. West Australian Petroleum Pty Ltd Report (unpubl.).
- PLAYFORD P E & LOWRY D C 1966. Devonian reef complexes of the Canning Basin, Western Australia. Geological Survey of Western Australia Bulletin 118.
- PLAYFORD P E & RUDDOCK I 1985. Discovery of the Kimberley goldfield. Journal and Proceedings of the Royal Western Australian Historical Society 9, 76–106.
- PLAYFORD P E & WALLACE M W 2001. Exhalative mineralization in Devonian reef complexes of the Canning Basin, Western Australia. *Economic Geology* **96**, 1595–1610.
- Read J F 1973a. Carbonate cycles, Pillara Formation (Devonian), Canning Basin, Western Australia. Canadian Petroleum Geology Bulletin 21, 38–51.
- Read J F 1973b. Paleo-environments and paleogeography, Pillara Formation (Devonian), Western Australia. Canadian Petroleum Geology Bulletin 21, 344–394.
- SMITH D N, PLAYFORD P E & WILLIAMS F B 1957. Oscar Range reef complex, Fitzroy Basin, Western Australia. West Australian Petroleum Pty Ltd Report (unpubl.).
- TEICHERT C 1939. Nautiloid cephalopods from the Devonian of Western Australia. *Journal of the Royal Society of Western Australia* 25, 103–121.
- TEICHERT C 1941. Upper Devonian goniatite succession of Western Australia. *American Journal of Science* 239, 148–153.
- TEICHERT C 1943. The Devonian of Western Australia, a preliminary review. *American Journal of Science* 241, 69–94; 167–184.
- Teichert C 1947. Stratigraphy of Western Australia. AAPG Bulletin 31, 1–70.
- TEICHERT C 1949. Stratigraphy and palaeontology of Devonian portion of Kimberley Division, Western Australia. Bureau of Mineral Resources Report 2.
- Wade A 1924. Petroleum prospects, Kimberley District of Western Australia and Northern Territory. Commonwealth of Australia, Parliamentary Paper, Melbourne.
- WADE A 1936. The geology of the West Kimberley District of Western Australia. Freney Kimberley Oil Company Report (unpubl.).
- Won M-Z 1997. Review of the family Entactiniidae (Radiolaria) and taxonomy and morphology of Entacliniidae in the Late Devonian (Frasnian) Gogo Formation, Australia. Micropaleontology 43, 333–369.
- WRAY J L 1967. Upper Devonian calcareous algae from the Canning Basin, Western Australia. *Professional Contributions of the Colorado School of Mines* 3.

Received 1 October 2013; accepted 5 November 2013

Recent mega-tsunamis in the Shark Bay, Pilbara, and Kimberley areas of Western Australia

P E PLAYFORD

Geological Survey of Western Australia, 100 Plain Street, East Perth, WA 6004, Australia. 🖾 phil.playford@dntp.wa.gov.au

Very large blocks of calcrete, thought to have been the products of mega-tsunamis, lie on flat karstified calcrete surfaces behind coastal cliffs in the Shark Bay area and on Barrow and Legendre Islands. Some of these blocks weigh more than 700 t and are the largest such blocks known in the world. They are much too large to have been transported by cyclones. Other mega-tsunami deposits are known from the Kimberley, where they include large blocks of Proterozoic siliceous sandstone and mafic igneous rocks. The extremely jagged nature of the ria Kimberley coastline may have resulted, at least partly, from erosion by repeated impacts by mega-tsunamis, over millions of years. The tsunami deposits at Barrow and Legendre Islands include closely packed oyster shells, as encrustations on boulders of calcrete and small boulders composed of the shells alone. Two samples of oyster shells from Legendre Island, and seven from Barrow Island, have been radiocarbon dated as 2895 and 3777 years BP (Legendre Island) and 3498 to 5444 years BP (Barrow Island). The tsunamis that struck the Kimberley coast have not been dated, but are thought to have been repeated many times during the past few million years, associated with seismic activity along the Sunda and Banda Arcs of Indonesia. The origins of mega-tsunamis that impacted on the coast from Shark Bay to the Pilbara are uncertain. They are presumably too far away from the Sunda and Banda Arcs for earthquakes there to have been responsible, and it seems more likely that they originated from large-scale slumping of sediment on the continental slope (possibly initiated by earthquakes) or local faulting. Other less likely origins are underwater volcanism or asteroid impacts in the Indian Ocean.

KEYWORDS: Banda Arc, earthquake, neotectonics, radiocarbon dating, submarine slumping, Sunda Arc, tsunami.

INTRODUCTION

My interest in tsunami deposits began in 1977 when travelling in a small boat beside Legendre Island off the Pilbara coast. Many large blocks of limestone could be seen lying above low cliffs at the north end of the island, and it seemed possible that they had been thrown there by a large tsunami. In 2009, when sailing near Koks Island in Shark Bay, big limestone blocks could be seen lying on the flat surface of the island, and it seemed that these too could have been products of a large tsunami (Playford 2013). Furthermore, on several voyages along the Kimberley coast, during 2006–2010, evidence could be seen to indicate that mega-tsunamis had hit that coast many times in the recent past.

It was not until 2010, while conducting field work for a bulletin on the geology of Shark Bay, that it was feasible to investigate the deposits in the Shark Bay area. Subsequently, similar deposits were examined along the Pilbara and Kimberley coasts (Figures 1–3).

These mega-tsunami deposits are among the largest known in the world, and in the Shark Bay and Pilbara areas they are thought to have resulted from mega-tsunamis that tore away large blocks of Pleistocene calcrete from the tops of low coastal cliffs, carrying them up to several hundred metres inland. Radiometric dating of oyster shells from Legendre Island indicates that one such mega-tsunami occurred about 2900 years ago. The Kimberley deposits contain large blocks of Precambrian silicified sandstone and mafic igneous rocks.

Several authors have previously recognised tsunami deposits along the Western Australian coast, including Scheffers *et al.* 2008 who described deposits at Quobba Point that are also discussed here. Several publications on West Australian tsunami deposits (including Burbidge & Cummins 2007; Burbidge *et al.* 2008; Nott 2004; Nott & Bryant 2003) have described other tsunami deposits along this coast, but most of those deposits contain blocks that are much smaller than those recorded here.

Many publications have discussed issues involved in distinguishing between tsunami and storm deposits (including Nott 2003 a, b; Nott & Bryant 2003; Burbidge & Cummins 2007; Goto et al. 2011; Imamura et al. 2008; Sheffers et al. 2010; Paris et al. 2011; Nandasena et al. 2011; Goff & Chagué-Goff 2014). Goto et al. (2011) reported field evidence from Okinawa that recent storm waves there have lifted 100 t boulders over a reef and up onto cliff tops as much as 15 m high. They also drew attention to other accounts of storm waves pushing boulders weighing as much as 235 t. On the other hand, Nott & Bryant (2003) concluded that storm waves could barely move boulders weighing 20 t, and boulders heavier than that could only be lifted and transported by tsunami waves. No authors have claimed that blocks as large as those described here (weighing up to 700 t) could have resulted from storms rather than tsunamis. Nevertheless, Goff & Chagué-Goff (2014) have claimed that none of the deposits described by these authors in Western Australia should be interpreted conclusively as tsunami deposits, as they could have resulted from intensive cyclones. I disagree with this conclusion, but as their paper only came to my attention when the present

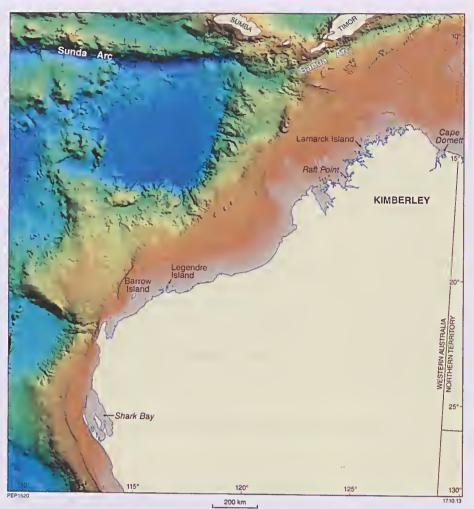


Figure 1 Map of part of Western Australia and its adjoining offshore area, from Geoscience Australia's map 'Surface Geology of Australia', showing the submarine topography and locations of mega-tsunami deposits in the Shark Bay, Barrow Island, Legendre Island, and Kimberley areas.



Figure 2 Map showing localities between the Zuytdorp Cliffs and Legendre Island where boulder deposits were emplaced by mega-tsunamis that hit the coast a few thousand years ago.

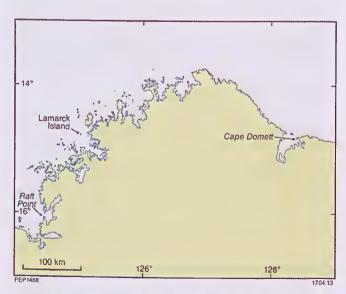


Figure 3 Map of the Kimberley showing the extremely jagged nature of the coast and the locations of photos included in the text. This jagged coastline may have partly resulted from repeated impacts by mega-tsunamis, over millions of years.



Figure 4 'The Block', situated beside the west coast of Dirk Hartog Island, 6.5 km southwest of Cape Inscription. This calcrete block measures $10.5 \times 8 \times 4 \text{ m}$, and is estimated to weigh at least 700 t. It was derived from the top of the shoreline cliff and thrown by a mega-tsunami about 15 m above sea level and 120 m behind the cliff.



Figure 5 Aerial view of a group of closely spaced imbricate calcrete blocks, on the west coast of Dirk Hartog Island, 15 km south-southwest of Cape Inscription, looking north. The largest block measures $13 \times 7.5 \times 3$ m, and weighs about 700 t. These blocks rest on a strongly karstified calcrete surface behind a cliff about 5 m high. They slope away from the coast, and were oriented in this way by the powerful backwash that followed the tsunami.



Figure 6 View of several of the calcrete blocks shown in Figure 5, showing their strong imbrication, sloping east, away from the coast, as a consequence of the backwash that followed the tsunami. Note the wedge shapes of the blocks, which resulted from abrasion as each block was pushed across the karstified land surface by the powerful backwash. Photo by Shaun Coldicutt.



Figure 7 Aerial view looking south over Cape Inscription on Dirk Hartog Island, (beside the place where Dirk Hartog landed in 1616), showing many angular slabs of calcrete (calcretised eolianite) lying on the cliff slope and at its base. These boulders are thought to have been dislodged by a mega-tsunami. Note that the numbers of blocks at the base of the cliffs decrease moving south from the headland.

paper was at the proof stage, it is not practicable to discuss the issues they raised in more detail.

Burbidge *et al.* (2008) pointed out that Western Australia has experienced five significant tsunamis in historic times. The largest, resulting from the 2006 Java earthquake, had a runup (height reached above sea level) of 9 m. Campers at Steep Point (at the northern end of Edel Land Peninsula) were lucky to escape, uninjured, from this tsunami. Burbidge *et al.* also reported that as a result of the Boxing Day Tsunami of 2004 (which originated at the northwest end of the Sunda Arc),

bathers beside some Western Australian beaches were dragged out to sea, but all managed to survive.

DIRK HARTOG ISLAND

Many boulder deposits that resulted from two or perhaps three tsunamis are recognised along the west coast of Dirk Hartog Island (Figures 4–6). They include huge blocks of limestone (calcrete), weighing many hundreds of tonnes. The largest of the blocks, known colloquially as 'The Block', is situated 6.5 km southwest of Cape





Figure 8 Photos taken in 1910 (top) and 2010 (bottom) of part of the scarp at Cape Inscription, looking north. They show large blocks of calcrete, up to several metres across, jumbled together at the foot of the cliff, and a thick calcrete layer at the cliff top. These large blocks have not moved during the past 100 years, despite many tropical cyclones having passed over or near Cape Inscription during that period. The SS Minilya, a State steamship last used there in 1910, can be seen in the top photo, which was taken by Adjee Cross.



Figure 9 Weathered boulders of calcrete on the west side of Dirk Hartog Island, about 200 m from the cliff face and 20 m above sea level. This deposit is thought to have resulted from a tsunami older than that responsible for the large boulders shown in Figures 4–6.



Figure 10 A deposit of small boulders, beside the coast south of Cape Inscription, that may have resulted from a very recent tsunami, although a severe storm could have been responsible.



Figure 11 Aerial view looking southwest over Koks Island, showing scattered boulders lying on the flat karstified surface. A large block lies perched on top of the cliff at the south end of the island. These blocks are thought to have been wrenched by a mega-tsunami from the two U-shaped re-entrants on the north side of the island.



Figure 12 Blocks of limestone thrown up by a mega-tsunami behind the low shoreline cliff at Point Quobba.



Figure 13 Composite air photo of Barrow Island showing the locations of oyster-shell samples collected from tsunami deposits, the radiocarbon ages of which are listed in Table 1.

Inscription (Figure 4). It measures $10.5 \times 8 \times 4$ m and is estimated to weigh at least 700 t. The mega-tsunami that carried these blocks is thought to have been at least 20 m high, with a runup on the land of more than 30 m, reaching hundreds of metres inland.

Calcrete blocks of comparable dimensions to 'The Block' are known at other places behind coastal cliffs along the northwest coast of the island. These blocks were torn from the cliffs and carried inland. At one place on the west side of the island there is a conspicuous group of closely spaced, wedge-shaped, imbricate blocks, sloping east, away from the coast (Figures 5, 6). Those blocks must have been thrown inland by the tsunami and then dragged back, towards the sea, by the huge backwash that followed. Abrasion of these blocks on the rough karstified calcrete surface resulted in their wedge shapes, with the upper surfaces dipping away from the sea. Such large-scale imbrication, thought to have resulted from the backwash of a tsunami, has not been reported elsewhere in the world.

Where the coastal cliffs are higher than about 15 m, blocks thought to have been dislodged by one or more mega-tsunamis have not been carried over the cliffs, but have remained on the cliff slopes or rest jumbled together at their base (Figures 7, 8). Although some of the blocks at those places could have resulted from normal subaerial collapse, most are probably tsunami-derived.

Deposits of smaller and more weathered boulders (maximum about 3 m across), extend as far as 200 m from the cliff face and about 20 m above sea level (Figure 9). They are thought have resulted from an earlier megatsunami, even larger than the one discussed above.

Another deposit of much smaller boulders occurs close to the coast, up to about 2 m above sea level, southwest of Cape Inscription (Figure 10). It must be younger than the other deposits described above. The boulders, measuring up to $2.3 \times 1.5 \times 0.5$ m, and weighing as much as 3 t, are very angular and unweathered. This deposit may have resulted from a very recent tsunami, much smaller than the other two. However, a major cyclone cannot be ruled out as the source, because of the relatively small size of the boulders that the deposit contains.

Some sandy deposits, thought to be tsunami-derived, are situated near the north coast of the island. Those deposits are up to 30 m above sea level, and contain large molluscs and small clumps of corals. Corals from one of these clumps have been radiocarbon dated as 4004±41 years BP. In contrast, a *Tridacna* (giant clam) shell in these sandy deposits returned a date of 38 522±605 years BP (Table 1), illustrating one of the problems involved in dating tsunami deposits. The organism in this shell must have died that long ago, before being swept up by a recent tsunami.

Photographic evidence shows that large boulders at the foot of the cliff at Cape Inscription, thought to have been dislodged from the calcrete layer at the top of the cliff by a mega-tsunami, have not moved during the past 100 years, despite at least seven tropical cyclones having passed over, or within 50 km of, Cape Inscription during that period (Figure 8). This observation is consistent with the interpretation that the large blocks there have been dislodged by a mega-tsunami rather than a storm.

DORRE AND BERNIER ISLANDS

Large blocks of calcrete commonly lie on subhorizontal surfaces behind coastal cliffs along the west coasts of Dorre and Bernier Islands, at places where the cliffs are not more than about 15 m high. These blocks have been carried as far as 300 m inland. Many very large blocks, apparently derived from the impacts of one or more mega-tsunamis, lie at the base of the cliffs or are plastered on the cliff slopes.

KOKS ISLAND

Koks Island is a small island (about 140×280 m), immediately north of Bernier Island. Many blocks, the largest measuring about $8 \times 6 \times 4$ m, and weighing about 500 t, rest on a flat calcrete surface about 10 m above sea level. One block lies perched on top of the cliff at the

Table 1 Results of radiocarbon dating of tsunami deposits on Dirk Hartog, Legendre and Barrow Islands.

Sample no.	Locality	Description	Elevation (approx)	Age (years BP)
135221	Dirk Hartog Island 697952E 7180228N	Clump of coral over red sand	30 m	4004 ± 41
135219	Dirk Hartog Island <i>Tridacna</i> shell 695968E 7177900N		27 m	$38\ 522 \pm 605$
135239	Legendre Island 482630E, 7749047N	Small block of oyster shells	4 m	2895 ± 35
135240	Legendre Island Larger block of oyster shells 482630E, 7749047N		4 m	3777 ± 40
135270 (3A)	Barrow Island Oyster shells encrusted on block of calcrete 5 m 325470E, 7697835N		5 m	5444 ± 37
135271 (3B)	Barrow Island 325470E 7697835N			4586 ± 37
135272 (6A)	Barrow Island 336760E 7713650N	Block of oyster shells	3 m	5245 ± 38
135273 (6B)	Barrow Island 336760E 7713650N	Block of oyster shells	3 m	3498 ± 36
135274 (8A)	Barrow Island Oyster shells encrusted on block of calcrete 8 m 325530E 7697960N		8 m	4091 ± 39
135275 (8B)	Barrow Island 325530E 7697960N	, , , , , , , , , , , , , , , , , , , ,		4652 ± 28
135 277 (8D)	Barrow Island Oyster shells encrusted on block of calcrete 325530E 7697960N		8 m	4571 ± 41

Analyst: University of Waikato Radiocarbon Dating Laboratory



Figure 14 Boulders of calcrete about 7 m above sea level on the west coast of Barrow Island, interpreted to have been derived from a mega-tsunami. Photo by Russell Lagdon.



Figure 15 Boulder of calcrete encrusted with closely packed oyster shells, on the west coast of Barrow Island. The oysters grew into pre-existing karst holes on the block, pointing to its complex history, as discussed in the text.

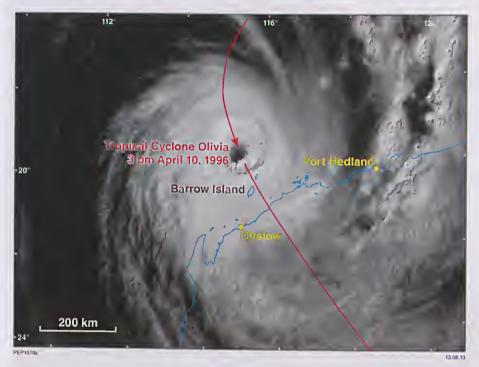


Figure 16 Image showing the path of Cyclone Olivia, an intense tropical cyclone that passed close to Barrow Island on April 10, 1996, generating the largest wind gust ever recorded on earth.

south end of the island. These blocks have apparently been derived from two U-shaped indentations in the cliff at the north end of the island (Figure 11).

On early charts of Shark Bay this island is labelled as 'Koks Island (boulders)', no doubt because the blocks on the flat top of the island are very conspicuous when viewed from a ship.

ZUYTDORP CLIFFS

No deposits that can unequivocally be interpreted as tsunami deposits have been identified along the Zuytdorp Cliffs. Those cliffs constitute a fault-line scarp that extends for nearly 200 km between Kalbarri and Steep Point (Playford *et al.* 2013). The cliffs, from 30 m to 260 m high, are too high to have allowed blocks of limestone to be carried up and over them by a mega-

tsunami. However, it is possible that many of the boulders lying on or below the cliff slopes have been dislodged by mega-tsunamis. Moreover, some sandy deposits on top of cliffs about 30 m high along this coast contain many marine shells and have hitherto been interpreted as Aboriginal kitchen middens (Morse 1988; Playford 1996). However, it seems possible that they are instead tsunami deposits, a hypothesis that remains to be tested in the field.

POINT QUOBBA

Large blocks of calcrete and calcretised eolianite rest on flat, bare, karstified calcrete surfaces behind coastal cliffs about 5 m high, on the mainland coast and a small island at Point Quobba, near the north end of the Shark Bay (Scheffers *et al.* 2008) (Figure 12). The largest block on the

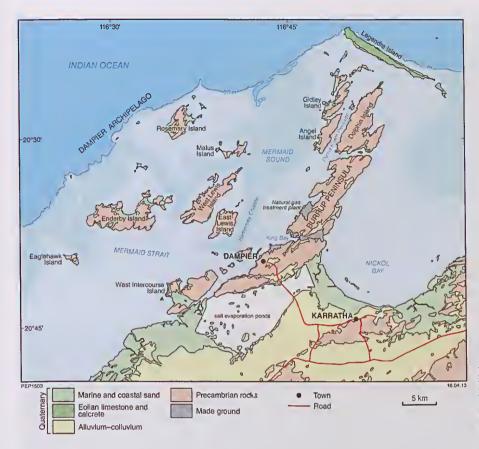


Figure 17 Geological map of the Burrup Peninsula area, showing the locations of Legendre Island, the towns of Karratha and Dampier, and the LNG facility.



Figure 18 Aerial view looking north over the northwest end of Legendre Island, showing large calcrete blocks deposited by a mega-tsunami about 2900 years ago, resting on a strongly karstified calcrete surface.



Figure 19 View on the ground of the large blocks of calcrete shown in Figure 18, lying on a strongly karstified calcrete surface. The largest of these blocks, on the skyline, is 12.5 m long.



Figure 20 Aerial view of part of the northwest coast of Legendre Island, showing sculpting of the cliff face attributed to one or more mega-tsunamis, with many blocks of calcrete lying scattered over the land surface and extending up to 300 m behind the cliff.

mainland is estimated to weigh about 70 t, only one tenth of the size of the largest blocks on Dirk Hartog Island. The smaller size of the blocks at Point Quobba can be explained by the fact that the tsunami wave in reaching there had passed over water much shallower than on the west side of Shark Bay, and this shallowing had reduced the size of the tsunami.

Scheffers et al. (2008) described several tsunami deposits on the west coast of Australia between Cape

Range and Point Quobba. They recorded blocks at Point Quobba that were torn from coastal cliffs and the adjacent sea floor and carried more than 200 m inland and 5–7 m above sea level. Some blocks derived from the sea floor are extensively bored by bivalves and the bivalve shells have been radiocarbon dated as 610–1670 years BP (Scheffers *et al.* 2008). Those authors also determined that at least one earlier tsunami event had occurred in that area, about 5700 years ago.



Figure 21 A column of silicified sandstone in a fault zone near Cape Domett, looking south, showing two reddishorange boulders of silicified sandstone perched near the top of the column, about 9 m above ground level and 12 m above sea level. They may have been deposited there by a mega-tsunami that moved from the north.



Figure 22 Boulder deposit on the east (lee) side of Lamarck Island. The boulders in this deposit are thought to have been torn from the west coast of the island and carried to this site by a mega-tsunami.

BARROW ISLAND

Barrow Island is the site of a producing oilfield, and a major liquefied-natural-gas (LNG) facility is now being built there to process gas from Chevron Australia's gasfields west of the island (Figure 13). A two-day visit was made to the island in May 2013, accompanied by Russell Lagdon, Environment Manager of Chevron.

Boulder deposits occur at various localities above and below coastal cliffs along the west coast of the island (Figures 14, 15). They consist of calcrete blocks up to 5.2 x 2.5 x 2.0 m in size and about 60 t in weight. Some blocks are encrusted with closely packed oyster shells; others consist entirely of such shells. The calcrete boulders are significantly smaller and more eroded, and appear to be older than those on Legendre Island and in the Shark Bay area. Oyster shells were collected for radiocarbon analysis at three localities. They returned ages of 3498 to 5444 years BP (Table 1). There is no clear explanation for such a large range in dates, but perhaps they point to at least three mega-tsunamis that occurred about 3500, 4100 and 5250 years BP. More detailed field work and radiocarbon datings will be needed to resolve this issue.

Some of the oyster encrustations are on pre-existing boulders of karstified calcrete, and the oyster shells extend into karst holes on those boulders (Figure 15). These boulders may have been carried onto the sea floor by the backwash of an earlier tsunami, then encrusted by oysters, and finally thrown up by another tsunami. It seems that the history of these tsunami deposits is very complex.

The edge of the continental shelf west of Barrow and Legendre Islands forms a steep scarp (Fig. 1). This is due to periodic collapse, possibly associated with faulting (Hengesh *et al.* 2013), and the resulting slides may have been responsible for the mega-tsunamis that are evidenced on those islands.

It is important to note that on 10 April 1996 an intense tropical cyclone, Cyclone Olivia, passed over Barrow Island (Figure 16). The strongest gust of wind ever recorded on earth (408 km/hour) was registered on the island during the passage of that cyclone (Courtney et al. 2012). Despite its extreme strength, this cyclone had no discernible effects on existing boulder deposits, nor is it known to have resulted in any new boulder deposits (Russell Lagdon pers. comm. 2013).

LEGENDRE ISLAND

Legendre Island, 15 km long and up to 1.5 km wide, is situated off the Pilbara coast, north of the Burrup Peninsula and near the towns of Dampier and Karratha, some 700 km north-northwest of Shark Bay (Figure 17). Huge blocks of calcrete rest on a flat calcrete surface in the north and northwest parts of the island (Figures 18–20), behind a jagged coastline of coastal cliffs thought to have been sculpted by mega-tsunamis. The blocks may be the products of one or more mega-tsunamis, but it is not known whether they were contemporaneous with any of those that struck Barrow Island and the coast of Shark Bay.

The largest of the calcrete blocks on Legendre Island

measures 12.5 m x 5 m x 4 m, is estimated to weigh more than 600 t, and lies about 8 m above sea level. These huge blocks must have been torn from the low cliffs along the north and northwest coasts of the island. Smaller blocks of oyster limestone also occur in the deposits, and these were apparently derived from oyster ridges that fringed shoreline platforms on the north side of the island. Two samples of the oyster blocks have been radiocarbon dated as 2895 and 3777 years BP (Alan Hogg pers. comm. 2010) (Table 1). The younger of those dates, rounded to 2900 years, may be the approximate date of the last tsunami, but many more dates are needed to test that conclusion.

KIMBERLEY COAST

Many deposits containing large blocks of silicified sandstone are present along the ria ('drowned') Kimberley coast, and are interpreted to have resulted from mega-tsunamis (Figures 1, 3, 21-24). The presence of such deposits is not unexpected in view of the proximity of the Kimberley to one of the world's most active seismic zones, the Sunda Arc beside Indonesia (Figure 24) (Hengesh et al. 2010). The adjoining Banda Arc is much less active, but large earthquakes do occur there periodically. At their closest, these arcs are less than 500 km from the Kimberley, and large earthquakes originating there can be expected to have generated tsunamis that may have had important roles in sculpting the jagged Kimberley coast. A mega-tsunami caused by a large earthquake along the closest parts of those zones could reach the Kimberley in about an hour. The same mega-tsunami, with progressively decreasing strength, would take more than two hours to reach the Pilbara and three hours to reach Shark Bay.

ORIGIN OF THE MEGA-TSUNAMI DEPOSITS

It has not been possible to link mega-tsunamis in the Shark Bay area, Barrow Island and Legendre Island with any of those that struck the Kimberley. Although megatsunami deposits in the Kimberley area are likely to have been generated by earthquake activity along nearby parts of the Sunda and Banda Arcs, those arcs are thought to be too far away to have been responsible for the megatsunami deposits along the Pilbara and Shark Bay coasts. Perhaps the most likely explanation for the origin of those deposits is massive slumping of sediments from scarps along the edge of the continental shelf (Figure 1: Hengesh et al. 2012; Bondevic et al. 2013; Scarselli et al. 2013). Such slumping may have been initiated by local earthquake activity. Other possible explanations are local faulting or (less likely) underwater volcanism and asteroid impacts in the Indian Ocean.

HUMAN AND FAUNAL CONSEQUENCES

The mega-tsunamis responsible for the boulder deposits in the Shark Bay, Barrow Island, Legendre Island and Kimberley areas were probably the most catastrophic events to affect Western Australia during the past 6000 years. They may have caused the deaths of thousands of Aborigines and animals then living in coastal areas. An



Figure 23 Cliff face of a small island near Raft Point in the Kimberley, surrounded by a wide band of very large angular boulders of siliceous sandstone, thought to have been dislodged by mega-tsunami impacts.

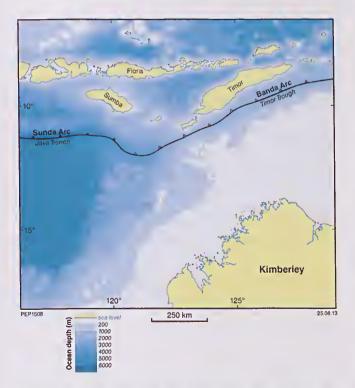


Figure 24 Map showing the Kimberley and parts of the Banda and Sunda Arcs, beside the Indonesian Archipelago. The intricately sculpted ria coastline of the Kimberley may have resulted from repeated impacts by mega-tsunamis resulting from earthquakes along the Sunda and Banda Arcs.

Aboriginal account of a 'big wave' that swept across the Montgomery Islands (in the Kimberley), probably during the early 20th century, is thought to have killed about 300 Aborigines, with only two survivors (Playford *et al.* 2013).

Another mega-tsunami could strike the coast of Western Australia at any time, although it may not eventuate for thousands of years. If such an event were to be repeated now, it would have devastating consequences for communities, towns and industries in some coastal areas.

ACKNOWLEDGEMENT

This paper includes many illustrations from Playford *et al.* (2013), and is published with the permission of the Director, Geological Survey of Western Australia.

REFERENCES

Bondevic S, Mangerud J, Dawson S, Dawson A & Lohne Ø 2003. Record-breaking height for 8000-year-old tsunami in the North Atlantic. *Eos* 84, 289–300.

Burbidge D. & Cummins P R 2007. Assessing the threat to Western Australia from tsunami generated by earthquakes along the Sunda Arc. *Natural Hazards* 43, 319–331.

Burbidge D, Cummins P R, Mleckzo R & Thio H K 2008. A probabilistic tsunami hazard assessment for Western Australia. *Pure and Applied Geophysics* **165**, 2059–2088.

- COURTNEY J, BUCHAN S, CERVENY R S, BESSEMOULIN P, PETERSON T C, RUBIERA J M, TORRES J, BEVAN J, KING J, TREVEN B & RANCOURT K 2012. Documentation and verification of the world extreme gust of wind record: 113.3 ms⁻¹ on Barrow Island, Australia, during passage of tropical cyclone *Olivia*. Australian Meteorological and Oceanographic Journal 62, 1–9.
- GOFF J & CHAGUE-GOFF C 2014. The Australian tsunami database: a review. *Progress in Physical Geography* **38**, 218–240.
- GOTO K, MIYAGI K, KAWANA T & IMAMURA F 2011. Emplacement and movement of boulders by known storm waves field evidence from the Okinawa Islands, Japan. *Marine Geology* 283, 66–78.
- Hengesh J V, Dirstein J K & Stanley A J 2012. Seafloor geomorphology and submarine landslide hazards along the Continental Slope in the Carnarvon Basin, Exmouth Plateau, North West Shelf, Australia. APPEA Journal 2012, 493–512.
- Hengesh J V, Dirstein J K & Stanley A J 2013. Landslide geomorphology along the Exmouth Plateau continental margin, North West Shelf, Australia. Australian Geomechanics Society 48(4), 71–92.
- HENGESII J, WYRWOLL K-H & WHITNEY B B 2010. Neotectonic deformation of northwestern Australia: implications for oil and gas development. Proceedings of the 20th Annual Australian Earthquake Engineering Society Conference, Perthhttp://www.aees.org.au/Proceedings/2010_Papers/22-Hengesh.pdf
- IMAMURA F, GOTO K & OHKUBO S. 2008. A numerical model for the transport of a boulder by tsunami, *Journal of Geophysical Research* 113, C01008, doi:10. 1020/2007JC004170.
- Morse K 1988. An archaeological survey of midden sites near the Zuytdorp wreck, Western Australia. Bulletin of the Australian Institute for Maritime Archaeology 12, 37–40.
- Nandasena N A K, Paris R & Tanaka N 2011. Reassessment of hydrodynamic equations: minimum flow velocity to initiate boulder transport by high-energy events (storms, tsunamis). Marine Geology 281, 70–84.
- Norr J 2003a. Tsunami or storm waves? Determining the origin of a spectacular field of wave-emplaced boulders using

- numerical storm surge and wave models and hydrodynamic transport equations. *Journal of Coastal Research* 19, 348–356.
- Note J 2003b. Waves, coastal boulder deposits, and the importance of pre-transport settings. *Earth and Planetary Science Letters* **210**, 269–276.
- Norr J 2004. The tsunami hypothesis comparisons of the field evidence against the effects on the Western Australian coast of some of the most powerful storms on earth. *Marine Geology* 208, 1–12.
- NOTT J & BRYANT E. 2003. Extreme marine inundations (tsunamis?) of coastal Western Australia. *Journal of Geology* 111, 691–706.
- Paris R, Naylor L A & Stephenson W J 2011. Boulders as a signature of storms on rock coasts. *Marine Geology* 283, 1–11.
- PLAYFORD P E 1996. Carpet of Silver, the wreck of the Zuytdorp. University of Western Australia Press, Perth.
- Playford P E 2013. Recent mega-tsunamis in the Shark Bay, Pilbara and Kimberley areas of Western Australia. Western Wildlife 17(4), 1, 4, 5.
- PLAYFORD P E, COCKBAIN A E, BERRY P F, ROBERTS A P, HAINES P W & BROOKE B P 2013. The geology of Shark Bay. Geological Survey of Western Australia Bulletin 146.
- Scarselli N, McClay K & Elders C 2013. Submarine slide and slump complexes, Exmouth Plateau, NW Shelf of Australia. *In:* Keep M & Moss S J (eds) *The Sedimentary Basins of Western Australia IV*, pp. 1–20. Proceedings of the Petroleum Exploration Society of Australia Symposium, Perth WA, 2013.
- Scheffers A, Kelletat D, Haslett S, Sander S, Scheffers S R & Browne T 2010. Coastal boulder deposits in Galway Bay and the Aran Islands, western Ireland. Zeitschrift für Geomorphologie 54, Suppl. 3, 247–279.
- Scheffers S R, Scheffers A, Kelletat D & Bryant E A 2008. The Holocene paleo-tsunami history of West Australia. *Earth and Planetary Science Letters* 270, 137–146.

Received 11 September 2013; accepted 6 November 2013 (note added in proof 9 June 2014)

Stromatolite research in the Shark Bay World Heritage Area

L B COLLINS 1* & R J JAHNERT 2

- ¹ Department of Applied Geology, Curtin University, GPO Box U1987, Perth 6845, Australia.
- ² Petrobras Company, Avenida Chile 65, Rio de Janeiro, 20031912, Brazil.
- * Corresponding author: 🖾 L.Collins@curtin.edu.au

Three decades after declaration of World Heritage status for Shark Bay new research findings are being reported on the specialised microbial habitats that characterise its hypersaline settings, the composition of microbial communities, tidal flat evolution, stromatolite geochronology and subtidal microbial systems. In the stable, semiarid and evaporative setting within the intertidal-subtidal environment the microbial ecosystem is trapping, binding and biologically inducing carbonate precipitation within laminated stromatolites, non-laminated thrombolitic forms and cryptomicrobial non-laminated forms. Filamentous microbes constitute the dominant group in the blister, tufted and smooth mat types, and coccoid microbes dominate the pustular, colloform and microbial pavement deposit types. Detailed georeferenced substrate mapping has revealed extensive subtidal microbial deposits occupying ~300 km² of the total Holocene 1400 km² area of Hamelin Pool. The microbial pavement covers 227 km² of the subtidal substrate, which together with columnar structures reveals a subtidal microbial habitat that occupies an area several times larger than the area of the intertidal deposits. Oldest dated stromatolite heads are 1915 14C years BP, and the overall system was deposited in two stages: the first between 2000 and 1200 and the last from 900 years BP to the present. Slow accretion rates vary from less than 0.1 to 0.5 mm/year. Different internal fabrics were constructed according to their position in relation to the littoral zone by distinct microbial communities, and lateral fabric relations have been established. Evidence of shallowing-upward fabric sequences of microbial origin reflects relative falling sea levels during the late Holocene and is likely useful in ancient environmental interpretation. A new substrate map and depositional history for this distinctive microbial habitat has established the significance of subtidal structures and emphasises the geoscientific importance of Hamelin Pool, especially with respect to early life studies and ancient analogues for understanding microbial activity, deposit characteristics, fenestral fabrics and distribution.

KEYWORDS: fabrics, geochronology, Holocene, microbial mats, stromatolites, subtidal microbialites.

INTRODUCTION

Since the existence of stromatolites in Shark Bay first became known in the 1950s there has been a developing interest by researchers in characterising the systems in the unique hypersaline conditions of Hamelin Pool and adjacent embayments (Figure 1), by marine geoscientists, biologists and others. The progress of this work is briefly summarised by Jahnert & Collins (2012 pp. 1-3), Burne & Johnson (2012) and Playford *et al.* (2013).

The purpose of this paper is to summarise the key findings of geoscientific investigations during 2008–2012 that concentrated on several aspects considered important among the wide opportunities for investigations of what is a remarkable occurrence of hypersaline microbial systems. The research was partly driven by a need to broaden the database required for ongoing management of the microbial and related assets of the Hamelin Pool Marine Nature Reserve and nearby areas in the Shark Bay embayments. Some of the questions addressed concern the nature of microbial tidal flats in areas of reduced salinity; the distribution of microbial habitats, substrates and fabrics on the tidal flats of Hamelin Pool; the chronology of stromatolite development; and investigations of the subtidal microbial habitats in Hamelin Pool. This summary draws on recently published detailed research accounts, particularly Jahnert & Collins (2011, 2012, 2013) and Jahnert *et al.* (2012).

METHODS

Regional mapping using remote sensing and ground-truth transects, shallow coring and sampling, and laboratory analysis were employed to map tidal flats, and marine embayments in order to document microbial habitats (Jahnert & Collins 2012, 2013).

Georeferenced maps were created using ESRI's ArcGIS, high resolution (50 cm/pixel) Shark Bay orthophotos and aerial photos (1:25 000 scale). A Multibeam survey was undertaken with the Department of Transport (DoT), Western Australia, focusing on the measurement of the depth and physical characteristics of the substrate along pre-defined transects. Submarine videos were recorded during marine investigations, and subtidal samples of microbial structures were collected in partnership with the Department of Conservation (now Department of Parks and Wildlife) which managed vessels and divers. A Differential Global Positioning System (DGPS) was used to record transect positions and high-resolution elevations (±5 cm) across tidal flats. Underwater videos were produced using drop-down video-camera, by diving or with cameras attached to the side of the vessel.



Figure 1 Hamelin Pool, L'Haridon Bight and Henri Freycinet embayment at Shark Bay, Western Australia. The image (from Geoscience Australia) shows the locations of Nilemah, Garden Point and Rocky Point.

Sampling involved limited collection of microbial heads from shallow depths by snorkelling and by scuba diving in the deeper portions. A taxonomic study of cyanobacteria was performed in the Microbiology Department at the Federal University of Rio de Janeiro, Brazil. Chemical analysis of microbial sediment and water samples involved X-ray fluorescence spectroscopy (XRF), inductively coupled plasma (ICP) optical emission and mass spectrometry, produced by Ultra Trace Analytical Laboratories, WA, and Petrobras S.A., Research Centre. 14C ages were obtained by the Radiocarbon Dating Centre of the Australian National University. Carbon and oxygen isotopes from sediment samples were analysed by the Federal University of Sao Paulo (USP). X-ray diffraction (XRD) techniques were used to characterise the crystallographic structure and recognise mineralogical constituents of sediment, and were performed at Curtin University. Scanning electron microscopy (SEM) was conducted at Curtin University.

ENVIRONMENTAL AND GEOLOGICAL SETTING

The Shark Bay embayments (Figure 1) are situated on the central west coast of Australia, and are dominated by a semiarid setting and subtropical conditions which are favourable to carbonate secreting organisms and communities. Shark Bay Marine Park is separated into three major embayments: Freycinet, L'Haridon Bight and Hamelin Pool. Freycinet embayment in western Shark Bay maintains the best connection with northerly oceanic waters so that, despite the high evaporation, salinity is metahaline (40-56: Logan & Cebulski 1970). Hamelin Pool, the easterly embayment, has restricted oceanic water influx and hypersaline waters (56-70), and progressively decreases in salinity to the north towards the tidal exchange channels crossing Faure Barrier Bank. L'Haridon Bight embayment contains metahaline conditions in the north and hypersaline waters to the

south. Tidal flats bordering the Shark Bay embayments have low substrate gradients (20–150 cm/km) with shallow and restricted water circulation, resulting in hypersaline conditions and microbial deposits that are widespread as mats or small elongate structures and discrete columns.

Shark Bay has three distinct geomorphic provinces; a western limestone terrain (Edel Province) which includes Dirk Hartog Island; a central Peron Province with characteristic red dune terrain, and an eastern limestone terrain which comprises the hinterland, the Toolonga Province. The geographic features of Shark Bay are controlled tectonically by a regional normal fault system of north-south orientation which intersects a northnorthwest-south-southeast oriented fold system responsible for confining the bays to the subsiding tidalchannel, tidal-flat, storm-beach and beach-ridge environments (Hocking et al. 1987). Two pre-Holocene marine transgressions are recorded. The Bibra Limestone ('Bibra Formation' of Logan et al. 1970; amended by van de Graaff et al. 1983), formed during the Bibra marine phase, is estimated to have been deposited during the last Pleistocene interglacial (MIS 5e) high sea-level stand at 120-130ka (van de Graaff et al. 1983; Hocking et al. 1987).

The Holocene sedimentary sequence was subdivided into five sedimentary units, based on their lithological variation, vertical and lateral relations and mapability: (i) Hamelin Coquina; (ii) Intertidal Veneer; (iii) Sublittoral Sheet; (iv) Bank Unit; and (v) Basal Sheet, which is located on the embayment plain (Logan et al. 1974b), where water depth is 10 m maximum. These sediments are dominantly organosedimentary in character and lithotypes in the peritidal zone can be broadly categorised into either microbialites or coquinites. The microbialites have been examined in many studies (Logan 1961, 1968; Davies 1970a, b; Playford & Cockbain 1976; Playford 1979, 1990; Logan et al. 1970, 1974b; Burne & James 1986; Burne & Moore 1987; Burne 1992; Burns et al. 2004; Dupraz & Visscher 2005; Reid et al.2003; Papineau et al. 2005; Burne & Johnson 2012; Jahnert & Collins 2011, 2012, 2013). The most recent review of the Shark Bay microbialites demonstrates that they exist in the form of subtidal pavements, subtidal microbial lithoherms of varying morphotypes and intertidal mats (Jahnert & Collins 2011, 2012, 2013). Their distribution is extensive, occupying nearly half the benthic substrate of Hamelin Pool (Jahnert & Collins 2011, 2012, 2013).

Shark Bay's recent geological past is characterised by three distinct marine transgressions, during the last part of the Quaternary as part of glaciation/deglaciation climate changes (Logan et al. 1974b; Jahnert & Collins 2011, 2012). These events are preserved in marine carbonate sequences that outcrop along the Shark Bay shoreline (O'Leary et al. 2008). The three drowning events correlate well with the polar ice core records and represent a 100 000 year frequency signal of advance and retreat of the sea. Slowly falling sea level (regression of 2 m) over the last 6000 years has been an important control on salinity increase, decline of seagrass banks (with the exception of the Faure Sill in the metahaline northern Hamelin Pool), stromatolite and tidal flat development, as well as basinward growth (progradation) of coquina coastal ridge systems (Jahnert et al. 2012). The spectacular stromatolite occurrences seen on intertidal surfaces in coastal settings have largely been stranded as sea level has declined, so that subtidal stromatolites (at depths 0–7 m below LWL) comprise much of the present-day microbial habitat.

RESULTS

Tidal flats in contrasting salinity settings

In a comparative study of tidal flat evolution in Shark Bay, three tidal flats (Figure 1) from contrasting salinity settings were evaluated (Jahnert & Collins 2013) to assess the role that salinity has played in their evolution, and to describe any contrasting characteristics in microbial mat and stromatolite occurrence and distribution. Hamelin Pool is a hypersaline embayment surrounded by extensive tidal flats: Gladstone, Hutchinson and the study site at Nilemah. Other nearby tidal flats located in L'Haridon Bight (transitional between hypersaline and metahaline conditions) and Henri Freycinet embayment (metahaline) are Rocky Point and Garden Point, respectively; these were also colonised by microbial communities, but under slightly different environmental conditions and timing. Whereas Nilemah is a northfacing embayment marginal to the Hamelin basin, both Garden and Rocky Point tidal flats are semi-isolated from their embayment waters by coquina barrier ridges.

Falling sea levels during the late Holocene led to establishment of coquina barriers and development of small, semi-barred tidal flats at various sites in the Shark Bay embayments, and establishment of areas suitable for microbial communities (Figures 1, 2). Such spit ridge accretion is usually controlled by south to north winddriven longshore currents for north-south oriented shorelines which dominate the embayments, but tidally constructed ridges often develop with north to south orientation, depending on coastal facing. The northfacing Nilemah embayment is partially enclosed by storm ridges with southwest and southeast transport directions on opposite shorelines. A combination of shallow conditions, low gradients (frequently 20 cm/km) and microtidal conditions controls the development of elevated salinities favourable for microbial colonisation in these settings.

The tidal flat environment has been colonised by microbial communities specialised in surviving at specific water depths, where a delicate balance between tidal energy, waves, exposure time and water depth results in accretion or erosion (Logan et al. 1974a, b) (Figure 3). Low water energy associated with high evaporation rates, sediment pattern and space creation are the key elements for sediment accretion in Shark Bay. Bacteria take advantage of diurnal tidal currents and waves that slowly cover the very flat area, supplying sediments and a habitat for microbes that are still adapting and expanding, producing carbonate by trapping and binding particles, biologically inducing carbonate precipitation and being lithified by aragonite cement. Cyclic tidal fluctuations also play a part in microbial distribution.

Hot summer temperatures (around 40°C) and strong southerly winds (40 km/h) force water out of the tidal

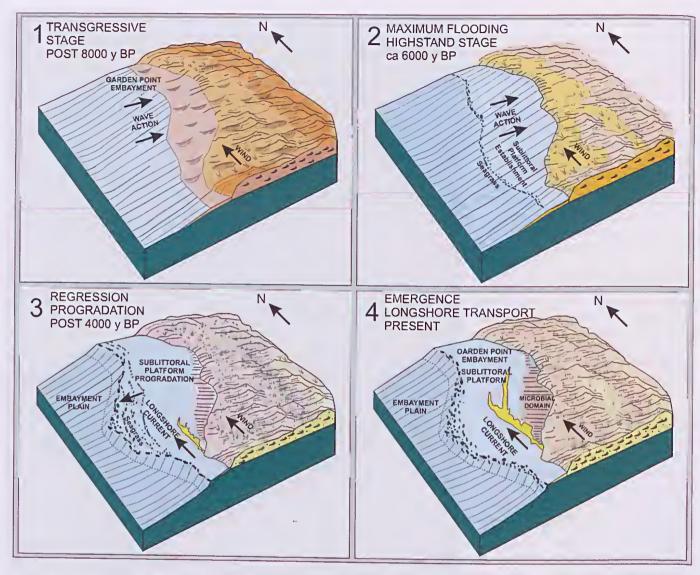


Figure 2 Morphological evolution proposed for the Garden Point embayment. Storm-wave activity was very important during the initial phase, while longshore currents, winds and tides were the morphological drivers during the late stages. Microbial activity started near 2300 years during the fall in sea level. (Jahnert & Collins 2013 figure 5).

flats, causing large areal exposure and desiccation of microbial deposits (pustular mainly), which shed globules of dead microbial mats. The distribution of sediments and microbial types on tidal flats such as at Garden Point reveals a sediment veneer made of carbonate, reflecting recent microbial activity within an environment that is frequently adapting to new conditions.

Six different microbial deposit types were recognised (Figure 4), mapped and sampled. Principal development and occurrence of mats is concentrated in the intertidal zone at Garden and Rocky Point and as additional microbial structures at Nilemah in the subtidal zone (Jahnert & Collins 2013). The supratidal zone does not preserve or generate extensive mats due to strong erosional processes, constant sediment movement and adverse conditions of temperature. Where bacteria survive it is in detached sites receiving a sporadic high-wind-driven water supply or abnormal tides. Microbial deposits in those sites are film and blister mats. Film mats are a black veneer normally covering lithified

surfaces exposed to the sun for long periods of time and belong to a novel type of halophilic archaeon, *Halococcus hamelinensis* sp. (Goh *et al.* 2006; Goh 2007).

Tufted mats occur in the upper intertidal zone, growing in scallops due to long filaments made by Lyngbya (Hoffman 1976) that exploit the ability to avoid direct contact with the ground and may block water and sediment inside the created relief. This mat normally develops over shallow muddy substrate where sediment maintains humidity landward of the pustular mat type. The intertidal zone is the growth domain of pustular mat spread as brown dark sheets of small bushes, inhabiting the upper intertidal to the upper subtidal zone. To construct a detailed map (Jahnert & Collins 2013), the term mini-pustular was introduced to refer to small bushes or pustules <1 cm in height and diameter. Pustular mats in the intertidal zone normally reach 3 cm high and >1 cm in bush diameter. In the upper subtidal zone, the high rate of peloid deposition discourages pustular growth that is still small in size (<1 cm high) and sparse, such as mini-pustular mat.

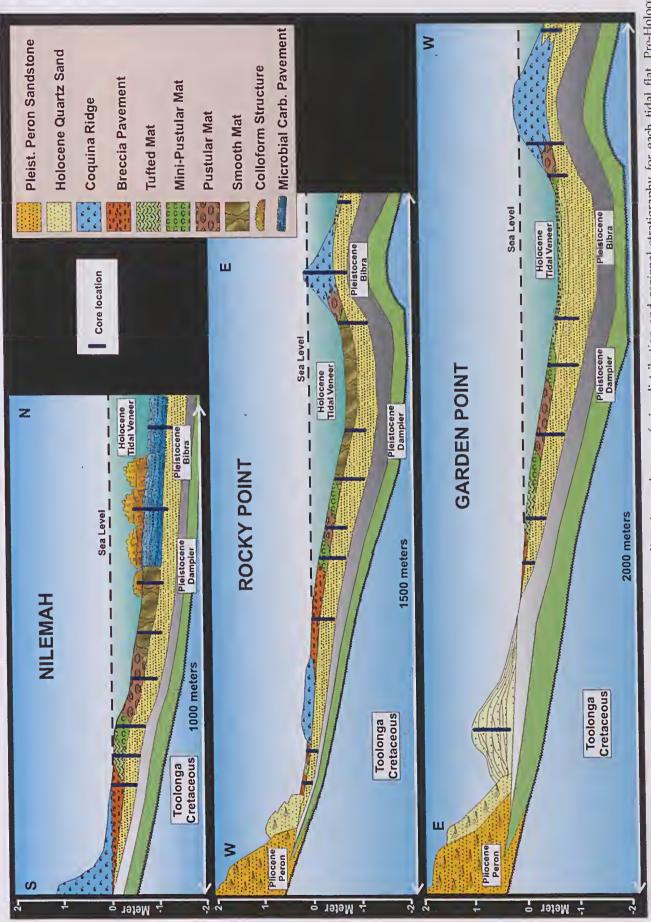


Figure 3 Cross-section of the three tidal flats showing sediment diversity and organofacies distribution and regional stratigraphy for each tidal flat. Pre-Holocene stratigraphy inferred from data in Logan et al. 1974b. (Jahnert & Collins 2013 figure 6).



Figure 4 Summary of the principal fabrics and external aspects of the microbial deposits for Nilemah, Rocky and Garden Point tidal flats (coin is 20.5 mm in diameter). (Jahnert & Collins 2013 figure 13).

In the upper subtidal zone, different bacteria such as *Schizothrix friesii* and *Microcoleus* produce a smooth mat composed of fine carbonate grains placed between vertical bacterial filaments that are able to permeate and trap sediments and produce laminar stromatolite fabrics. Garden Point includes a proximal pond where, in very calm water rich in sediment particles, a set of coarse laminar smooth microbial mats has developed. However, Garden Point, in contrast to the other tidal flats, is in the initial phases of establishing bacteria, and only the proximal substrate portion of the subtidal zone is colonised.

In the subtidal zone of Nilemah tidal flat, seaward of the smooth mat terrain, colloform microbial deposits (-0.5 to -1.5 m) develop as elongate structures followed by a tabular microbial carbonate pavement extending to deep subtidal zones (-1.0 to -6.0 m).

The improved knowledge of the nature and distribution of the tidal flat microbial deposits is documented in georeferenced maps (Jahnert & Collins 2013) of the sediments and organodeposits of Garden and Rocky Points. These are characterised by relatively extensive and prolific microbial activity during the last 2300 years, producing microbialites that are exposed in the supratidal zone. These are now subject to erosion, and are progressively colonising the subtidal zone as a consequence of sea level fall, although observations of recolonisation in the intertidal zone provides evidence of a recent short marine transgression (Jahnert & Collins 2013).

TAXONOMIC STUDIES

A taxonomic and phylogenic grouping was established based on microscopic characteristics of the dominant cyanobacteria on the surface of microbial mats or structures (Figure 5) (Jahnert & Collins 2013). Bacterial communities are responsible for the external and internal colours and morphologies of organosedimentary deposits. Sixteen species of cyanobacteria were identified. Ten species that belong to the Class Cyanophyceae, Order Chroococcales, live in coccoid colonies and have small spherical to oval forms arranged in envelopes of jelly-like mucilage, normally yellow to dark orange in colour. Another six species belong to the Class Hormogonae, Order Oscillatoriales; these filamentous bacteria with elongate formats are often surrounded by a sheath that contains many individual cells with colours ranging from dark green to light green and blue. Filamentous bacteria are the dominant group, producing blister mats (Microcoleus chthonoplastes), tufted mats (Lyngbya aestuarii, L. fragilis and Phormidium willei) and smooth mats (Schizothrix friesii and Microcoleus chthonoplastes).

Coccoid bacteria dominate the pustular mats (Gloeocapsa punctata, Chroococcus minimus, Entophysalis granulosa), colloform deposits (Entophysalis granulosa, Chroococcus turgidus, Gloeothece vibrio) and microbial pavement (Cyanosarcina thalassia, Chroococcus microscopicus, Entophysalis conferta). Diatoms including Navicula were identified in samples from smooth, colloform and microbial pavement, but despite the thick mucilage around the diatom cells, colonies of bacteria have been seen inside the extracellular polymeric secretions (EPS), and the process of organomineralisation appears to be driven by the bacteria even in diatom domains.

COMPARATIVE EVOLUTION

Table 1 is a summary of the contrasting properties of microbial mats and sediments within the three tidal flats studied (Jahnert & Collins 2013). While the intertidal microbial systems are similar, the destructive effects of bioturbation are more evident at Garden and Rocky Point

Table 1 Comparison between tidal flats, water salinity and the contrasting properties of microbial mats and sediments within the littoral zones (Jahnert & Collins 2013 table 1).

Tidal flat	Water salinity	Contrasting properties	
Garden Point	Metahaline to hypersaline	Microbial mats: pustular mat dominance; smooth mat only in restricted pond. Microbial sediments: carbonate veneer (30 cm max.) with significant influx of quartz sand. Subtidal zone: bioclastic-quartz sand sheets (proximal) and bioclastic seagrass banks (distal). Bioturbation: disturbs and reworks microbial mats. Sediment isotopes: concentrate in less positive values of δ^{13} C (+3.4 to +5.2) and δ^{18} 0 (+2.0 to +3.6) Onset of hypersalinity: coquina storm deposits dated 14 C 2050–2150 (±35 years)	
Rocky Point	Metahaline to hypersaline	Microbial mats: pustular mat domain intertidal zone and smooth mat in subtidal zone. Microbial sediments: carbonate veneer (50 cm max.) with influx of quartz sand. Subtidal zone: smooth mat (proximal) and bioclastic seagrass banks (distal). Bioturbation: disturbs and reworks microbial mats. Sediment isotopes: concentrate in intermediate values of δ^{13} C (+3.6 to +5.3) and δ^{18} 0 (+2.5 to +3.8) Onset of hypersalinity: coquina storm deposits dated 14 C 2420, 2830 and 3160 (±35 years)	
Nilemah	Hypersaline	Microbial mats: pustular mat domain intertidal and smooth, colloform and pavement in subtidal zon Microbial sediments: carbonate layer (1.30 m max.) and low influx of quartz sand. Subtidal zone: smooth, colloform structures and microbial pavement widespread. Bioturbation: limited by hypersalinity. Sediment isotopes: concentrate in more positive values of δ^{13} C (+4.0 to +5.9) and δ^{18} 0 (+3.0 to +3.0 Onset of hypersalinity: coquina storm deposits dated 14 C 4630 (±35 years)	

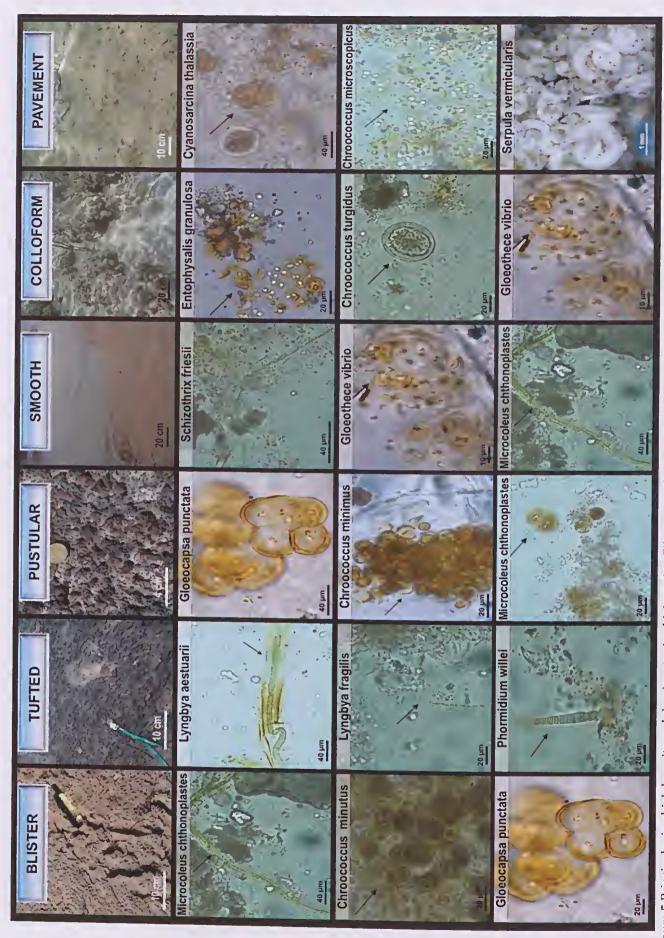


Figure 5 Principal microbial deposits and dominant microbial species. Filamentous bacteria dominate the blister, tufted and smooth mat environment and coccoid bacteria dominate the pustular, colloform and microbial pavement. (Jahnert & Collins 2013 figure 17).

than at Nilemah. Also, the subtidal smooth mats give way to seagrass banks offshore, whereas in the hypersaline Nilemah subtidal zone, colloform stromatolites and lithified bioclastic microbial pavement are widespread. The onset and duration of elevated salinities appears to be the driving mechanism for these differences. There is a chronological progression in the ¹⁴C age of coquina beach ridges from the least saline to the most saline conditions such that Garden and Rocky Point are relatively youthful, which likely explains the retention of seagrass banks, frequency of bioturbation, and lack of subtidal microbialites relative to the older, more hypersaline Nilemah embayment.

Hamelin Pool substrates and microbial distribution

Whilst previous research has documented specific tidal flats and localised features, the opportunity for a wider mapping of microbial substrates arose from the need for regional data, for World Heritage management. The microbial systems and related sediments of Hamelin Pool were mapped (Figure 6) using high-resolution orthophotos, GIS and supporting terrestrial and submarine ground truth information, and classified according to their regional occurrence and distribution within the hinterland, supratidal, intertidal and subtidal domains (Jahnert & Collins 2012) (Figure 7). More

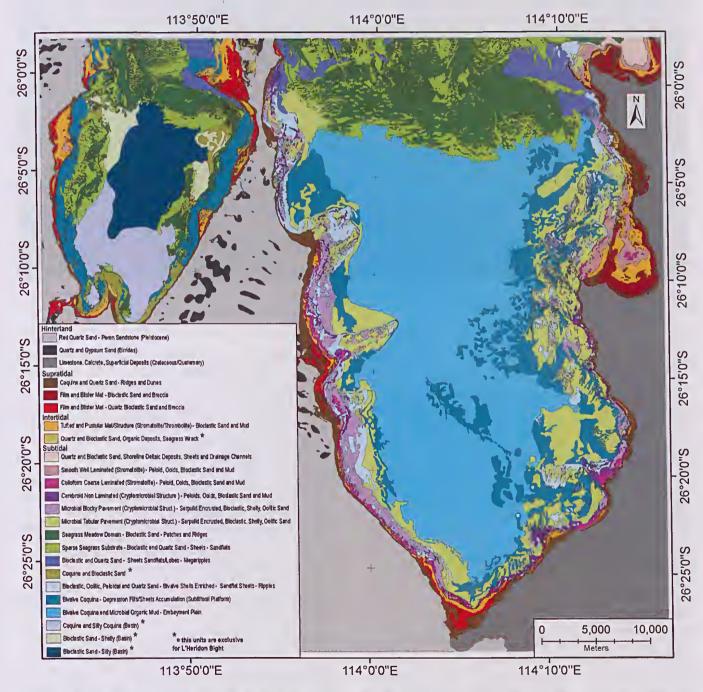


Figure 6 Hamelin Pool and L'Haridon Bight georeferenced sedimentary and organosubstrate map based on numerous coastal and marine ground truth traverses, video transects, aerial surveys, samples and interpretation of digital orthophotos.



Figure 7 Hamelin Pool microbial substrates.

recently mapping has been extended to cover L'Haridon Bight to the west of Hamelin Pool.

Hinterland deposits are composed of quartz sandstone (Peron Sandstone) that comprises most of the embayment margins. The Peron Sandstone is an eolian Pliocene-Pleistocene deposit generated during glacial phases (Butcher et al. 1984). Interdune depressions contain spherical and ellipsoidal depositional basins consisting of granular gypsum and quartz sediment fills, termed birridas. The eastern Hamelin embayment hinterland is dominated by limestone of the Toolonga Calcilutite (Cretaceous) and superficial Quaternary cover that includes calcrete, quartz sand, laterite, alluvial and colluvial deposits. The eastern flank also contains emergent shoals composed of oolitic limestones of the Carbla Oolite (Pleistocene) expressed as elongate bodies parallel to the paleoshoreline which is to landward of the present shoreline.

The supratidal zone is influenced by storms and abnormal tides and thus often exposed to erosional processes. Microbes survive in topographic lows and local depressions as detached sites of ephemeral mats which are only sporadically wet. These microbes are adapted to survive in high substrate temperatures and grow in blister, tuft or pinnacle forms. The supratidal

zone in Hamelin Pool occupies nearly 80 km², and contains two organosedimentary units which are exposed and prograding seaward, as described below.

The Hamelin Coquina, the upper unit of the Holocene system, is a supratidal beach ridge system which overlies thin Pleistocene units and the Pleistocene Bibra Formation and, as a consequence of sea level fall (Logan et al. 1974b), progrades toward the centre of the embayment over Holocene supratidal microbial deposits, as shore-parallel ridges above the normal spring high tide level. Bioclastic-oolitic/quartz sand and breccia occupy extensive areas between the coquina deposits and the area reached by normal tides. Breccia pavements (Figure 8H) occur as lithified crusts that developed over older microbial pavements and heads, generated by processes that include desiccation, cementation and disruption by gypsum crystallisation (Logan et al. 1974a, b).

Supratidal areas are the domain of film and blister microbial mats. Film mat refers to a black veneer that covers breccia clasts and lithified exposed material in sites that may have a connection with underground water or sites that receive any kind of water spray. Blister mats develop in flat muddy substrates that receive sporadic flooding and maintain humidity.

Intertidal organosediments occupy a relatively small area (22 km²) and accommodate extensive microbial mats and heads in shallow waters. The intertidal is a domain of pustular and tufted microbial deposits. Pustular mats spread as brown dark sheets of small colonies, inhabiting the upper intertidal to the upper subtidal zone and, depending on the substrate gradient, develop mats, ridge-rill or subspherical structures. Tufted mat occurs in the upper intertidal zone, growing in scallops that accumulate water and sediment within the created relief. Tufted mat normally develops over shallow muddy substrate, usually landward of pustular deposits.

Subtidal microbial deposits are extensive, occupying an area of ~300 km² of the total Holocene 1400 km² area of the Hamelin Pool Marine Reserve. Subtidal microbial deposits that grow as structures cover 54 km². Subtidal deposits were classified according to their actual microbial superficial dominance, although many structures were partially constructed in different conditions of sea level presenting internally different fabrics. Areas of Hamelin Pool lacking microbial carbonates are dominated by seagrass and related bioclastic and quartz sand, particularly located near the Faure Bank to the north of the embayment, and bivalve coquina, serpulids and algae with a superficial veneer of organic rich material spread over the 'Embayment Plain'. Mobile sheets of bioclastic and quartz sand occur in areas affected by strong tidal currents, such as the sublittoral platform and over the Faure Bank. The biosedimentary subtidal deposits (Jahnert & Collins 2011) are summarised below.

Laminated microbial smooth stromatolites composed of beige flat surfaces, occur as mats and buildups with internal fabric composed of flat subhorizontal millimetric laminae of fine-grained carbonate sediment interbedded with laminae of microbial organic matter, lithified as micrite laminae. Laminated microbial colloform stromatolites construct buildups of brown/yellow colours externally composed of small (1-5 cm) hemispherical globular shapes rich in fine-grained peloids. Internal layers are composed of ooids/peloids that alternate with thin laminae of lithified micrite generating a coarse laminoid wavy internal fabric with subhorizontal elongate voids. Non-laminated cryptomicrobial cerebroid structures are the deepest subtidal buildups growing as domical, ridge-like or prismatic elongate morphologies of white to cream colours. Cerebroid structures contain superficial cavities with coarse grains/fragments and are often bored by bivalves. Patches of micrite are sparse in a bioclastic/oolitic sediment rich in bivalve shells, serpulids and colonised by algae.

Cryptomicrobial tabular pavement occurs as flat substrates which are being lithified as bioclastic grainstone and includes *Fragum* serpulids, microgastropods, foraminifera and algae. Cryptomicrobial blocky pavement is similar to the facies described above but is disrupted/reworked producing partially to wholly disconnected blocks, rich in *Fragum* bivalve shells and colonised by serpulids along basal surfaces.

Bioclastic/oolitic/peloidal sand occurs in the sublittoral region as a result of longshore currents and storm activity producing sand-floored depressions adjacent to microbial deposits. Bivalve coquinas constitute extensive deposits of *Fragum* bivalve shells, which inhabit the

sublittoral platform waters between -1.5 and -6 m. Bivalve shells are abundant in Hamelin Pool. Some of the disarticulated shells are swept into deeper portions of the bay, others fill depressions as gravel and a large number are transported shorewards and deposited in the supratidal zone by storms as exposed beach ridges. Bioclastic sand with variable quartz content comprises the substrate of seagrass domain in channels, patches or as ridges oriented east-west perpendicular to the tidal action. Bioclastic and quartz sand occurs in substrates colonised by seagrass but in disconnected sparse stands such as those found over Faure Bank, and bioclastic and quartz sand also occurs in shallow areas to the north on the Faure Bank where tidal velocity is amplified constructing channel lags, channel bars, subtidal deltas, and sand sheets with sand waves and megaripples. Bivalve coquinas with serpulids, algae and a superficial organic mud dominate the deeper portions in the Embayment Plain.

MICROBIALITES AND INTERNAL FABRICS

Distinct internal fabrics result from microbial processes of trapping and binding, microbially-induced carbonate precipitation, organic matter content, amount and type of sediment input, presence of voids, presence of skeletons, bioturbation and macropore orientation. Subtidal microbial carbonate deposits are designated as pustular, smooth, colloform, cerebroid and microbial pavement (Figures 8, 9). They have distinct internal fabrics, related to the dominant microbial communities (Burns *et al.* 2004; Allen *et al.* 2009; Jahnert & Collins 2012), their growth habits and environmental conditions.

Coccoid bacteria dominate the intertidal environment constructing pustular deposits with non-laminated clotted fabric and are appropriately designated thrombolite (Logan et al. 1974a p. 185). Coccoid bacteria also dominate the deep subtidal zone in colloform, cerebroid and microbial pavement, here producing coarse laminated stromatolites in colloform deposits and cryptomicrobial non-laminated carbonate in cerebroid and microbial pavement. Filamentous bacteria are the dominant group in smooth mats and heads in the subtidal zone producing carbonate structures with a fine laminoid fabric and characterised as stromatolite.

The organic matter that constitutes a considerable portion of the sedimentary fabrics is strongly modified when exposed to desiccation and oxidation, mainly by creating volumetric space, producing fenestral porosity (Logan *et al.* 1974a). In many cases, fenestral fabrics remain well preserved in the geologic record and are a distinctive characteristic of many rock sequences and their environments (Riding 1991; Walter 1999; Grammer *et al.* 2004).

Sediment of microbial origin (90 samples) from supratidal to subtidal zones submitted to mineralogic analysis by XRD revealed a predominance of aragonite in the carbonate fraction of 80–98%. Minor amounts of Mg-calcite and calcite and rare dolomite comprise the other carbonate minerals. Quartz is variable (10–40%) and higher in samples from the south and west of Hamelin Pool reflecting its proximity to the Peron Sandstone. Halite is minor (1–10%) and gypsum only occurs in supratidal samples (1–10%).

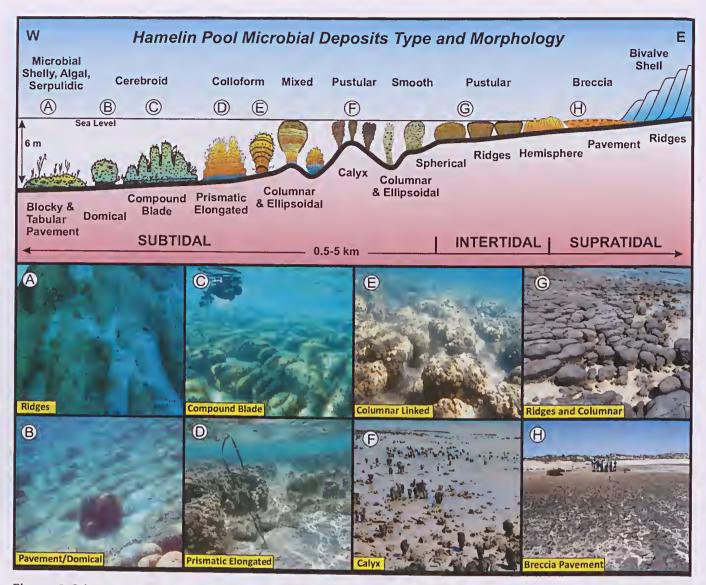


Figure 8 Schematic depositional model for microbial deposits in Hamelin Pool highlighting the distribution, characteristics and morphologies according to the tidal zones. (Jahnert & Collins 2012 figure 5).

Stable isotopes of $\delta^{13}C$ and $\delta^{18}O$ obtained from subtidal microbial carbonate sediment (12 samples) revealed positive values of carbon and oxygen isotopes. The overall $\delta^{13}C$ values vary between +4.46 and +5.88 while the $\delta^{18}O$ varies from +3.06 to +3.88. Smooth and colloform carbonates display the highest $\delta^{13}C$ values (+5.41, +5.67, +5.72 and +5.88). The isotopic relationships suggest that all the samples were deposited in a highly evaporative environment with extensive microbial activity.

GEOCHRONOLOGY

Nine microbial heads were analysed to determine ages and obtain growth rates. The sampling involved a careful selection of heads, collected, as far as possible, to cover the different microbial buildups occurring from the supratidal zone (head 1) to the subtidal zone in water depth of 4 m (head 9). The samples were projected onto a regional single transect (Figure 10) in order to permit a comparison between ages, depths, external morphologies and sizes.

The selected microbial structures display different

external morphologies, from columnar to domical and tabular (Figure 10) with external surfaces tending to dark colours in pustular and over shallow-water domains, presumably because of the microbial pigments present. Structures are predominantly composed of carbonate grains, bioclasts and micrite arranged in different fabrics, which likely represent the prevailing conditions at the time and so furnish an evolutionary chronological history when ¹⁴C dated. Bivalve shells and other visible coarse skeletal bioclasts (that could contaminate ages) were removed from samples subjected to ¹⁴C dating analysis. The samples were composed mostly of fine carbonate particles (mud and silt size), sampled at the top, middle and base of the heads, when possible, to establish a trendline of growth rates.

The high resolution ¹⁴C dating age values (Figure 10) for this collection are substantially older (1915–1680 years BP) when compared with the results obtained by Chivas *et al.* (1990), who recognised the interval of 1250–1000 years BP as the time of growth of the first stromatolites. Evidence of an earlier higher sea level than at present can be seen in head 1 (Figure 10) aged 1680 (base), 1300

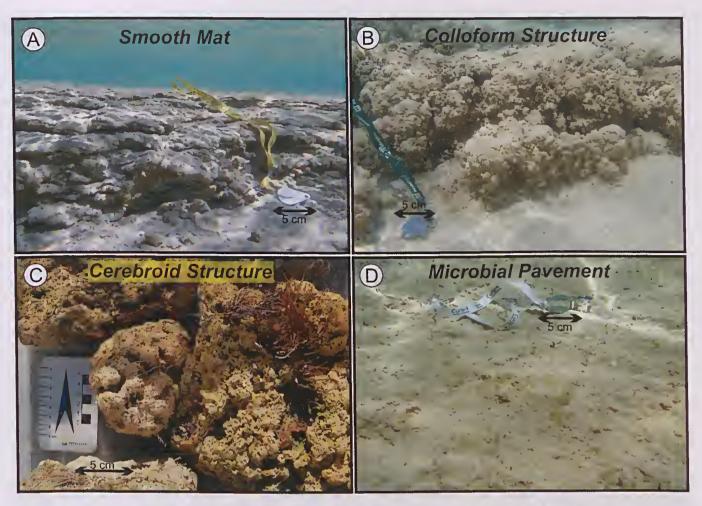


Figure 9 Principal microbial deposits and their external characteristics. (A) Well developed laminar fabric in smooth mat. (B) Colloform structures, external view (globular appearance; rich in fine carbonate particles). (C) Cerebroid structure; note convoluted external form with cavities, and algal ornamentation. (D) Microbial pavement; flat, lithified bioclastic carbonate with abundant bivalve shells, serpulids and soft-bodied algae. Sediment of microbial origin (90 samples) from supratidal to subtidal zones submitted to mineralogical analysis by XRD revealed a predominance of aragonite (80–98%) in the carbonate fraction. Minor amounts of Mg-calcite and calcite and rare dolomite comprise the other carbonate minerals. Quartz is variable (10–40%) and higher in samples from the south and west of Hamelin Pool reflecting Peron Sandstone proximity. Halite is minor (1–10%) and gypsum only occurs in supratidal samples (1–10%). (Jahnert & Collins 2012 figure 9).

and 1120 (top) years, located today in the supratidal zone, exposed 30 cm above mean sea level. Externally it has a columnar morphology characteristic of the subtidal zone and an internal vertical fabric sequence of cerebroid–colloform–smooth (base to top); reflecting a sequence of fabrics generated while submerged in the subtidal zone but at decreasing depths.

Accretion rates obtained from Shark Bay microbial structures are variable from <0.1 mm/year to little more than 0.5 mm/year highlighting how slow the process of stromatolite accretion is and how delicate is the microbial environment. The presence of stromatolite structures 1.5 m in height points to a higher accretion rate of 0.75 mm/year if using the same constructional age period of 2000 years. The relationship between interval accretion rates versus fabrics does not permit establishment of useful trends from the data available: however, the higher overall accretion rate values using trendlines indicate that subtidal colloform and cerebroid heads have faster

development. The ¹⁴C accretion rates obtained here (range <0.1–0.54 mm/year) have a greater spread when compared with values obtained by Chivas *et al.* (1990) who determined by ¹⁴C dating values between 0.1 and 0.34 mm/year, for microbial structures in Hamelin Pool. Playford & Cockbain (1976) after an investigation period of five years measuring growth rates (with non-corrosive nails) in heads of intertidal and subtidal zones of Hamelin Pool, confirmed that many stromatolites have reached a state of equilibrium, with no accretion but recorded one head with a maximum accretion rate of 1 mm/year.

MICROFABRICS AND CONSTRUCTIONAL MECHANISMS

Internal fabrics preserved in the microbial buildups vary significantly in Shark Bay denoting changes in environment and microbial ecosystems adapted to produce carbonate deposits in different water depths and

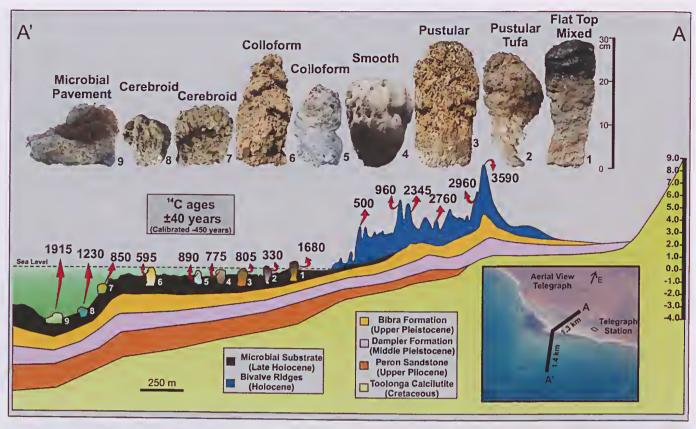


Figure 10 Regional cross-section based on DGPS (land) and multi-beam (water) surveys located north of Telegraph Station area with projected microbial samples and respective ¹⁴C ages calibrated by subtracting 450 years from the conventional ages. The stratigraphy is based on boreholes drilled over the ridge system (in blue) and is projected offshore. The supratidal Hamelin Coquina storm ridge transect (morphology and ages) is shown for comparative purposes. Note basinward (upper surface) ages; also relict, emergent head 1 at landward end of transect. (Jahnert & Collins 2012 figure 10).

environmental conditions which are characterised as follows.

Irregular clotted fabric originates from pustular thrombolitic deposits. Pustular deposits are the domain of coccoid cyanobacteria, characterised at the surface by thick brown mucilage produced by the copious amounts of a highly hydrated translucent gelatinous mucilage that undergo organomineralisation after periods of exposure (Golubic 1980, 1982) (Figure 11A). Micrite is generated also by the endolithic activity that fuses and micritises carbonate peloids (SEM images analysis).

Well-laminated (smooth) stromatolites are related to the activity of filamentous cyanobacteria responsible for producing exopolymers that trap sediment producing flat and slippery surface morphology (Figure 11B, 12A). The fabric reveals alternation of grain/bioclast-enriched laminae with peloidal organic-rich laminae generated during storms and subsequent quiescent periods.

Coarse laminoid (colloform) stromatolites develop in subtidal areas deeper than smooth domains, where fine carbonate particles are still available and the ecosystem can develop both vertically and horizontally as adequate space is available. Coccoid cyanobacteria and diatoms produce enough mucilage to trap and bind grains/bioclasts and presumably biologically induced mineralisation producing lithified laminae which are

sustained by vertically constructed lithified columns, leaving horizontal voids (Figure 11C).

Non-laminated cryptomicrobial (cerebroid) structures are the deeper subtidal buildups characterised by external irregular cavities that receive coarse material and are often bored by bivalves. The presence of a significant amount of *Fragum* bivalve shells, ooids and serpulids is a characteristic of these deposits. Lithification results from peloidal grain micritisation and fusion, dark micrite precipitation and fibrous aragonite cementation growing in pore spaces (Figure 11D). Cerebroid structures are a domain of coccoid cyanobacteria.

Microbial pavement refers to light grey cryptomicrobial carbonate deposits with tabular or blocky surface morphologies that are being lithified as bioclastic grainstone and includes skeletons of *Fragum erugatum* bivalves, serpulids, micro-gastropods and foraminifera. It is externally colonised by *Acetabularia* (calcified green algae), Fucales (brown algae) and Gigartinales (red algae).

Coccoid cyanobacteria dominate shallow ecosystems producing pustular deposits, followed by the filamentous cyanobacteria group that produce smooth mat and structures. The permanently submerged buildups, colloform, cerebroid and microbial pavement, represent an ecosystem dominated by coccoid cyanobacteria. In

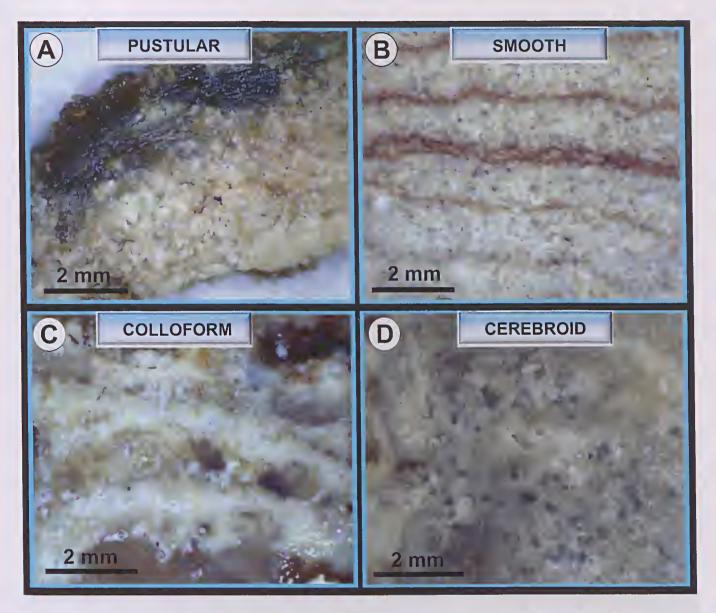


Figure 11 Macrophoto detail of the different fabrics that produce microbial buildups in Shark Bay. (A) Brown dark pustular with thick mucilage and carbonate particles (peloids) trapped. (B) Smooth internal fabric consisting of grain/bioclast-enriched laminae alternating with organic rich laminae with peloids. (C) Colloform coarse laminoid fabric with lithified micritic laminae interbedded with bioclastic and ooidal laminae, sustained by lithified columns constructed vertically, leaving horizontal voids. (D) Cerebroid internal fabric showing non-laminated micrite and bioclastic and ooidal grains. Serpulid exoskeletons are abundant inside the cerebroid fabric. (Jahnert & Collins 2012 figure 13).

water depths of -4 m the filamentous cyanobacteria *Phormidium hypolimneticum* and *Lyngbya fragilis* were detected in the surface of the microbial pavement living within the coccoid domain.

Subtidal microbial structures differ regarding their external morphologies and internal fabrics, which reflect sediment availability, bivalve skeleton supply, substrate morphology and depth, wave activity, tidal runoff, sea level and the microbial community that constructs deposits through different stages and processes of early (synsedimentary) diagenesis which interact as follows.

(1) Superficial micrite generation Precipitated micritic carbonate is a characteristic observed in SEM images and occurs within organic gel (EPS) and is related to the microbial communities (Figure 12A–C). Such organic

gels, which are recognised in hand sample and SEM, expand over the surface of structures, connect discrete particles, stabilise sediment and initially sustain the structure. The organic gel also surrounds bacterial filaments, connects material and apparently generates micrite, biologically inducing precipitation (Figure 12A). A detailed image shows a filamentous sheath surrounded by micrite particles generated within the organic gel (Figure 12B), and crystallisation of aragonite that also surrounds bacterial filaments (Figure 12C).

The process of grain accretion is driven by filamentous bacteria in the smooth mat domain and coccoid bacteria in the colloform, cerebroid and microbial pavement domains. Sediment accretion is undertaken mostly by cyanobacteria through photosynthetic production of

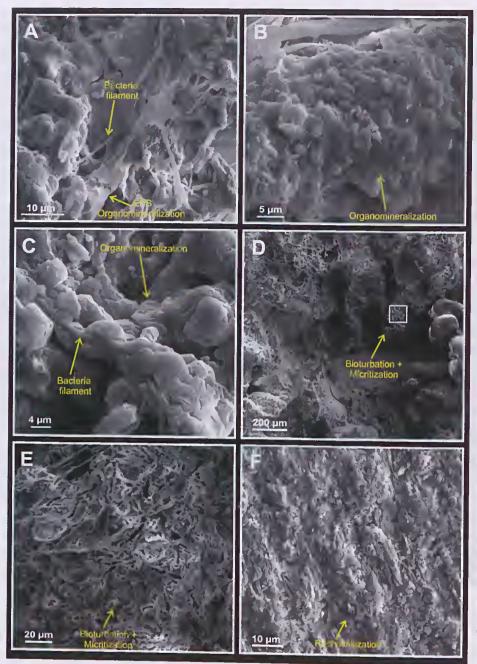


Figure 12 SEM photomicrographs from samples and thin-sections (coated with gold or platinum), showing the sequence of events that involves trapping and binding (stage 1) and organomineralisation in filamentous cyanobacterial domains (A-C) and (stage 2) activity of endolithic microbial bioturbation, micritisation and recrystallisation (D-F); the first stage 1 (A-C) reflects the activity of filamentous bacteria in smooth heads from living (dried) material from Nilemah. (A) The organic gel surrounds bacterial filaments, connects material and apparently is generating micrite. (B) Detail of filamentous sheath surrounded by micrite particles generated within the organic gel (probably EPS). (C) Superficial crystallisation of aragonite that also surrounds bacteria filaments. (D) Carbonate grains severely attacked by microorganisms that produce a honeycomb-like surface in ooids. (E) Detail of rugose surface with tunnels and light-coloured recrystallised microcrystals. (F) Soft peloid grains are micritised and fused obliterating peloid boundaries and producing an extensive new recrystallised micrite. Images from smooth head located at Nilemah and cerebroid heads at Carbla Point and south of Carbla Point. (Jahnert & Collins 2012 figure

exopolymer (Visscher et al. 2000; Reid et al. 2003; Dupraz & Visscher 2005) that traps and binds grains and particles and also attracts calcium ions to negatively charged sites (Pentecost 1991).

(2) Bioturbation, micritisation and recrystallisation Bioturbation, micritisation and recrystallisation (Figure 12D–F) produces grain fusion and recrystallised micritic layers responsible for indurated laminae between soft grainy/bioclastic sand in colloform and smooth heads and produces discontinuous patches of micrite in deeper cerebroid and microbial pavement structures. Carbonate grains are attacked by microorganisms producing a honeycomb-like surface in ooids (Figure 12D) creating a rugose surface with micro-canals and light coloured recrystallised microcrystals (Figure 12E). Soft grains of peloids are micritised and fused producing an extensive new recrystallised micrite (Figure 12F).

These processes are driven by microbial endolithic activity, with an estimated density of 200 000 bacteria/ mm² (Golubic 1982), driven by heterotrophic bacteria that penetrate carbonate grains and bioclasts for nutrition and protection (Campbell 1982) producing grain fusion, micritisation (Macintyre *et al.* 2000; Reid *et al.* 2003) and recrystallisation. The most frequent sources of organic carbon for the support of heterotrophic endolithic activity are the primary products of photosynthetic bacteria and organic matrix of skeletons (Campbell 1982).

(3) Pervasive micrite generation Occurrence of a last generation of micrite is visible in thin-sections and SEM distributed in all sediment generated, both surficially and within heads in aphotic zones, characterised as a dark cryptocrystalline and microcrystalline micrite, which fills spaces and envelopes grains and skeletons (Figure 13G–J). The micrite is characterised by an amorphous carbonate

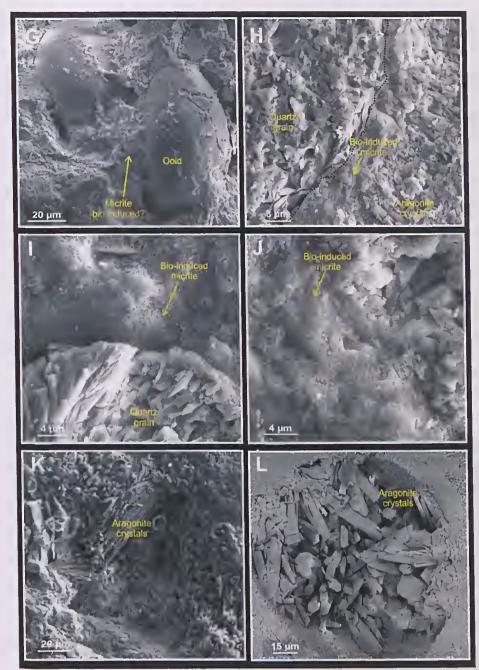


Figure diagenetic 13 Early mechanisms involved in microbial deposits, showing (stage 3) generation of organic micrite enveloping grains and bioclasts (G, H, L, I) and (stage 4) fibrous aragonite precipitation in void spaces (K, L). (G) Ooids grains connected with a fine texture micrite. (H-J) Details of fine texture micrite which precedes the last process of aragonite crystal growth. (K) Aragonite crystals arranged depending on the space available, as a pervasive crystal system or as microcrystals. (L) Welldeveloped aragonite needles inside larger voids. Images from cerebroid heads located at Carbla and south of Carbla Point. (Jahnert & Collins 2012 figure 15).

which in SEM resembles a texture of fine foam, distinct from other micrite generated by cyanobacteria or endolithic bacterial activity. Grains are connected and stabilised by this kind of micrite (Figure 13G) that reveals in detail (Figure 13H–J) a fine texture that always occurs before the last step of aragonite crystal growth. This micrite is responsible for most of the deeper water source of sediment stabilisation and is deposited presumably as a result of sulfate-reducing bacterial activity (Visscher *et al.* 2005).

(4) Fibrous aragonite precipitation Aragonite crystal growth in void spaces is the last diagenetic product during the construction of microbial structures. The process is recognised as an important step for the final stabilisation of sediment in the subtidal cryptomicrobial structures although it is almost negligible in shallow subtidal smooth domains. Aragonite crystals are

arranged depending on the space available, as a pervasive crystal system or as microcrystals (Figure 13K) and also well developed needles inside larger voids (Figure 13L).

When the relative abundance of specific microbial substrates is compared it is evident that the subtidal microbial habitat is far more widespread than previously known in Hamelin Pool, for example in comparison to the intertidal microbial substrate, and this will be explored in succeeding sections. The less saline L'Haridon Bight lacks subtidal microbial substrate and has remnant seagrass banks in less saline areas around its margins, a further contrast with Hamelin Pool from which sublittoral seagrass habitat is virtually absent. The Faure seagrass bank forms the northern barrier to both basins. The effect of late Holocene regression is also evident from the laterally extensive intertidal microbial

substrates on low-gradient tidal flats which record shoreline retreat, and the stranding of microbialites as sea level has fallen.

Hamelin Pool: microbial deposits and substrate morphology

The delicate balance between tidal energy, waves, exposure time and water depth results in sediment accretion or erosion in Shark Bay (Logan *et al.* 1974b). Low water energy associated with high evaporation, sediment supply and topography are key elements for sediment accretion. The gross morphology of microbial deposits is related to the interaction of these factors with the embayment coastal morphology and its related substrate gradient. The general coastal morphology of Hamelin Pool can be classified into three different types: headlands, bights and embayment tidal flats (Logan *et al.* 1974a; Hoffman 1976).

Headlands are characterised by steep gradients (Figure 14) of 4 m/100 m, where the substrate favours growth of submerged microbial deposits (up to 1.5 m high) as columnar, domical, conical and club-shaped morphologies. Intense activity of waves and tidal currents is responsible for erosional effects on the microbial structures, which often exhibit basal thin necks, tunnels, and other evidence of erosion. The high energy

of currents also supplies coarse carbonate grains and bioclasts that become trapped by microbial activity. Water depth controls the living microbial communities which respond with distinct communities, internal fabrics, external colours (pigmentation) and growth styles.

Bights are subtle re-entrants with gradients of about 2 m/km with microbial deposits forming mats or elongate structures and tabular microbial pavement in subtidal regions. The structures (about 50 cm height) have their long axes perpendicular to the shoreline and parallel to tidal current direction.

Embayments occur in re-entrants along the coast, normally protected by the presence of coquina barrier ridges. The tidal flats have low gradients of about 30–50 cm/km and produce extensive deposits of microbial mats. Because of sea level fall during the last thousand years the microbial system is adjusting its position seaward, so that landward areas are now exposed and under erosion producing brecciated microbial deposits, often expressed as breccia pavements.

Fluctuating tidal and wave energy controls the amount of carbonate particles available to be deposited and trapped by microbes which, depending on microhabitat, construct laminar or non-laminar fabrics (Figure 14). High-energy water near smooth and

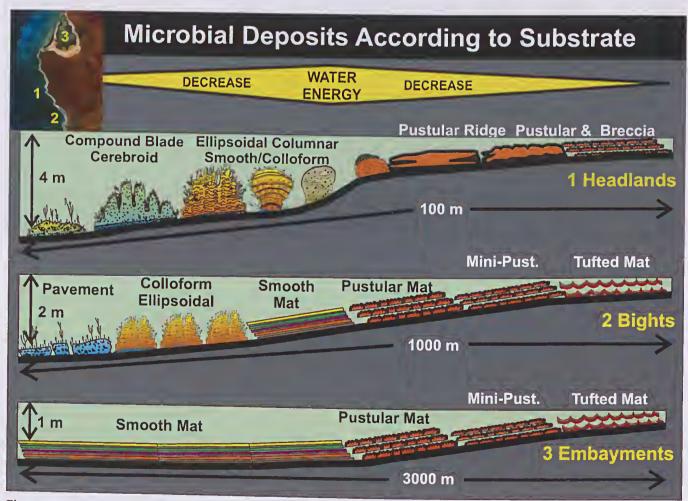


Figure 14 Microbial deposit morphologies and types according to the substrate gradient. Headlands have steep gradients with growing heads while embayments have low gradients and are colonised by widespread mats. (Jahnert & Collins 2012 figure 3).

colloform domains is rich in fine carbonate particles that, after storms, are slowly deposited supplying microbial communities with enough material to produce laminar fabrics. Deeper waters are depleted in fine carbonate particles and microbial communities stabilise sediment by inducing carbonate precipitation and trapping fine grains. Coarse particles such as bivalve shells and fragments, bioclasts and ooids are widely available and are deposited mainly during storms.

Hamelin Pool has an extensive sublittoral platform with a gently sloping top (0.5–3 m/km) and a more steeply sloping margin >4 m/km; this platform extends basinward to water depths as deep as 6 m.

Subtidal realm and subtidal microbial deposits

Submarine videos, photos, samples and bottom substrate profiles have provided substantial material which was used to identify, map and classify the morphology of microbial structures and their distribution in the subtidal areas, supporting the creation of georeferenced organosedimentary maps of Hamelin Pool and supplying accurate substrate elevations for each group of microbial structure type (Figure 7).

Colloform microbial deposits (-0.5 to -1.5 m) occur as beige to brown elongate prismatic, spherical and club-

shaped structures (long axis oriented parallel to tidal action) in the subtidal environment. Colloform deposits externally show small (1–5 cm) globular hemispherical forms rich in fine-grained peloids and ooids. Internally layers of grains (2-10 mm) alternate with thin laminae of lithified micrite generating a coarse laminoid internal fabric (Logan et al. 1974b) often with weak lamination (Hoffman 1976; Playford 1990). Lithification is promoted by micritic layers of bacterially induced mineralisation, fusion of peloids and aragonite cement. Colloform microbial deposits are the domain of Entophysalis, Chroococcus, Gloeothece cyanobacteria and diatoms (John 1993), that also provide shelter for many living eukaryotes such as Fragum bivalves (Logan et al. 1974b; Berry & Playford 1997), crustaceans, serpulids, microgastropods, foraminifera, Acetabularia, Fucales and Gigartinales).

Cerebroid microbial deposits (-1 to -2.5 m) are the deepest subtidal buildups occurring as domical, ridged or prismatic club-shaped morphologies of white to cream colours. The external appearance (Figure 15) resembles a cerebrum in a dorsal view with abundant spherical/elongate dark cavities distributed in a white to grey carbonate mass. Cerebroid structures have superficial cavities that contain coarse material and are often bored by bivalves. Internally pink patches or clots of micrite

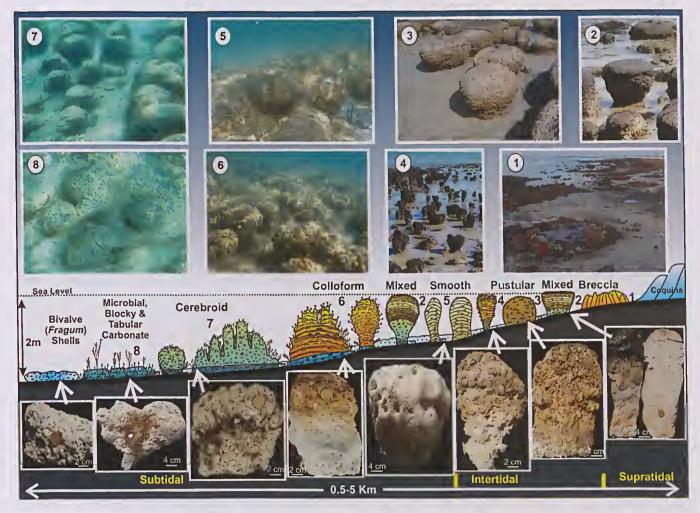


Figure 15 Microbial structure types at base with schematic fabrics and correspondent images taken in the field at Hamelin Pool, Shark Bay. (Jahnert & Collins 2011 figure 2).

occur sparsely around clusters of carbonate sand and shells or within bivalve concavity producing a non-laminated fabric (Figure 16). Bivalve shells of *Fragum erugatum* are abundant in these structures which dominate the subtidal habitat and consist of coccoid cyanobacteria: *Chrococcus microscopicus*, *C. giganteus*, *C. ercegovicii* and *Aphanocapsa litoralis* at the superficial photic zone.

Petrographic constituents are ooids, peloids, skeletons, bioclasts and quartz grains. Peloids and ooids are partially fused, micritised and burrowed, producing micrite patches that are sparsely distributed. A dark green late micrite infills cavities and envelopes grains suggesting an important role in sediment stabilisation. Serpulid skeletons, shell fragments and ooids show partial recrystallisation to phosphatic carbonate. Iron-rich carbonate in small amounts (<3%) and pyrite are present in ooids or internally on skeletons. Lithification results from grain micritisation and fusion, dark micrite precipitation and fibrous aragonite cementation growing in pore spaces.

Microbial pavement (-2 to -6 m) is a light grey microbial carbonate deposit with tabular or blocky surface morphologies being lithified to form bioclastic grainstone and includes *Fragum erugatum* bivalves, serpulids, micro-gastropods, foraminifera, *Acetabularia*, Fucales and Gigartinales. The abundance of *Fragum* and

serpulid skeletons is characteristic of these deposits that cover extensive areas of the subtidal platform. Dark green micrite as a product of organomineralisation coats grains and skeletons as a fundamental element connecting and stabilising sediment (sensu Riding 1991, 2000). Coccoid cyanobacteria Cyanosarcina thalassia and Chroococcus microscopicus dominate the superficial photic zone.

Based on analysis of data from habitat mapping, subtidal microbial structures from colloform and cerebroid types (Figure 16) are responsible for more than 70% of Shark Bay columnar structures. Colloform structures are as high as 1.5 m, often connected laterally forming extensive kilometric strips 50–500 m wide as reefs parallel to the coast, with cerebroid as the deeper buildups of 1 m maximum height. The microbial pavement is revealed as an important widespread microbialite (*sensu* Burne & Moore 1987) that is colonising and stabilising the substrate over the sublittoral platform of Hamelin Pool in water depths from 2 to 6 m.

MICROBIAL PROCESSES AND PRODUCTS

To produce stromatolites, thrombolites and cryptomicrobial structures in Shark Bay, bacteria take advantage of stressing environmental conditions that limit the attack of predators and competitors. Formation

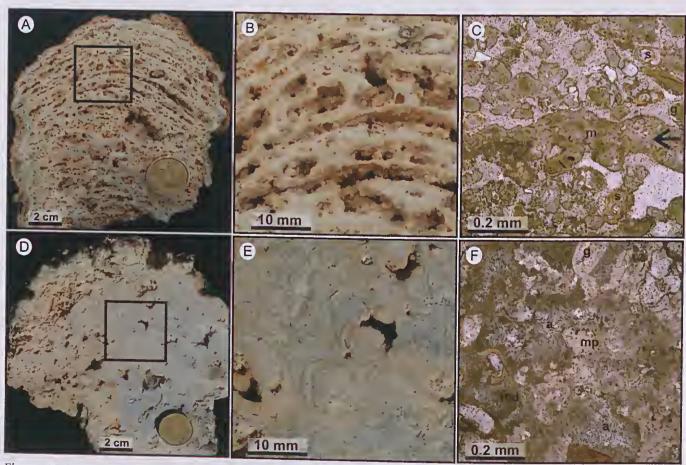


Figure 16 Comparison between the dominant subtidal microbial structures. (A) Colloform structure, with (B) detail of laminoid fabric and (C) photomicrograph showing subhorizontal laminae (arrow) of fused peloids: micrite (m), skeletons (s) and grains (g). (D) Cerebroid structure, with (E) detail of non-laminated fabric and (F) photomicrograph revealing patches of light-pink (mp) and a dark-green micrite (md), grains (g) and aragonite (a). (Jahnert & Collins 2011 figure 3).

of subtidal structures occurs through different stages and processes that interact as follows:

Sediment accretion is conducted mostly by cyanobacteria through photosynthetic production of exopolymer (Visscher et al. 2000; Reid et al. 2003; Dupraz & Visscher 2005) that traps and binds grains and particles and also attracts calcium ions to negatively charged sites (Pentecost 1985). Grain accretion is driven by filamentous bacteria in the smooth mat domain and coccoid bacteria in colloform and cerebroid domains. These bacterial communities along with diatoms produce volumes of exopolymers sufficient to connect, stabilise sediment and initially sustain the structure. As organic compounds and sulfate/sulfite are present, heterotrophic and phototrophic bacterial activity sponsors a further stage in evolution and growth of heads. Sulfate-reducing bacterial activity (Visscher et al. 2000; Dupraz & Visscher 2005; Baumgartner et al. 2006; Dupraz et al. 2009) is an important source of carbonate precipitation through induced-mineralisation which is also responsible for early lithification of the structures. Sulfate-reducing and sulfur-oxidising bacteria account for 66% of the total population of active bacteria in five samples of Shark Bay submitted to genomic DNA analysis.

Stabilisation of aragonitic micrite in laminae (colloform, smooth) or patches (cerebroid) occurs in peloidal layers submitted to a process of grain fusion and micritisation by endolithic bacterial activity of carbonate mineralisation. In colloform heads these fused micritised levels are responsible for indurated laminae between soft grainy material. In cerebroid heads the process is localised to some mottled portions leaving other patches (2–5 cm) of grainy friable sediment.

Generation of organic micrite, presumably as a result of sulfate-reducing activity produces a dark green microcrystalline micrite which fills spaces and envelopes grains and skeletons and is responsible for most of the deep-water source of sediment stabilisation. Aragonitic cementation subsequently occurs involving fibrous aragonite precipitation in void spaces.

A summary of subtidal morphology and fabrics is presented in Figure 9.

The importance of fusion of micritised grains as responsible for early lithification of microbial structures in Shark Bay has been previously recognised (Reid et al. 2003). Those authors have also described a subtidal microbial precipitate of unknown composition which has an originally laminated micrite infilled by an 'entophysalidacean species' that obliterates original lamination producing 'unlaminated stromatolites'. Our findings show cerebroid deposits form as widespread deeper subtidal microbial buildups with unlaminated fabric and patches of micrite, but apparently not as a result of disturbance of lamination. Laminated micrite is a characteristic of shallower waters in colloform and smooth mat domains rich in fine sediment available to be deposited and generate laminar fabric. Cerebroid heads are mostly constructed by coarse sediment forming a non-laminated fabric, because of the irregular surface morphology, intense bioturbation and restricted amount of peloidal particles available in deep subtidal domains.

The abundance of coarse coquina bound into cerebroid heads attests to the high availability of bivalve shells, the

dominant sediment type in the subtidal regions and periodic high storm energy to rework and redistribute coquina which is incorporated into these heads, as opposed to quiescent conditions of fairweather waves. In contrast, shallower microbial substrates trap and retain sand-size bioclasts and peloids in lower energy conditions in tidal flats.

The prolific subtidal cementation involves induced microbial mineralisation, grain fusion and aragonite precipitation occurring in a hypersaline setting where both carbonate saturation and microbial activity are significant. Throughout the Hamelin Basin and tidal flats alkalinity, salinity and Ca ion availability is high (pH 7.5-8.6, salinity 60-65 and Ca⁺⁺ 500-1080 mg/L) based on continuous measurements (48 hours) in southern Hamelin Pool. It is likely that these parameters may be related to depth, temperature, wave agitation and CO, content of waters, but a firm conclusion awaits future analysis. However, based on DNA/RNA organosediment measurements, the high degree of EPS biomineralisation as seen in SEM photomicrographs of cerebroid heads and relatively high positive values of $\delta^{13}C$ (> +4.2) and $\delta^{18}O$ (> +3.1) recorded in microbial sediment it is clear that microbial activity has a strong imprint on the subtidal facies.

STROMATOLITES, AGE, INTERNAL FABRICS AND REGRESSION

Distinct internal fabrics result from microbial processes of trapping and binding, carbonate-induced precipitation, organic matter content, amount and type of sediment input, presence of voids, presence of skeletons, bioturbation and macropore orientation. Subtidal microbial carbonate deposits are designated as pustular, smooth, colloform, cerebroid and microbial pavement (Figures 8, 9). They have distinct internal fabrics, related to the dominant microbial communities (Burns *et al.* 2004; Allen *et al.* 2009; Jahnert & Collins 2011, 2012, 2013), their growth habits and environmental conditions.

An interpretation of ages versus fabrics and water levels permits recognition of two stages of depositional growth; The first was between 2000 and 1100 years ago, a period when the shoreline shifted landward and buildups were developing as columnar, ellipsoidal, and spherical forms and as large microbial hemispheres (+2 m diameter) in the subtidal zone which remain partially exposed today in the supratidal/intertidal zone around Hamelin Pool. Evidence of this first event can be seen at the observation deck at Telegraph Station, where large microbial hemispheres and some columnar microbial structures are exposed near the shoreline. There is also evidence of old tidal flats exposed in the supratidal zone with microbial mats recognised at Nilemah and Hutchinson, some producing breccia pavements. The second phase of microbial carbonate deposition occurred from 900 years ago to the present day during the falling sea level (on the order of 1.5 m) to present level. During this second phase the microbial domain expanded considerably as the sublittoral platform became shallower and was marked by an increase in fine carbonate particles (peloids) responsible for deposition of the majority of laminated stromatolites. Holocene microbial structures record evidence of changing environmental conditions and water depth producing vertical depositional sequences, which represent shallowing-up sedimentary sequences.

The relationship between the internal fabric and the water depth where the microbialites are generated has been established. Non-laminated/disrupted cryptomicrobial fabrics with a high content of bivalve shells, ooids, and serpulids are characteristic of 'deep water' (-1 to -6 m) growth as buildups (cerebroid) or microbial tabular or blocky pavement. Coarse and fine laminoid fabrics correlate to shallower waters (-5 cm to

-1.5 m) rich in fine carbonate particles developing colloform and smooth structures and the shallow water (0 to -40 cm) is colonised by pustular deposits with internal irregular to clotted fabrics. These relationships (Figure 8) assist identification in columnar forms exposed today in the supratidal zone of distinct internal fabric sequences which are non-laminated at the base (cerebroid) followed by coarse laminated (colloform), well-laminated (smooth) and a flat eroded top with a dark film veneer. These fabric sequences represent a

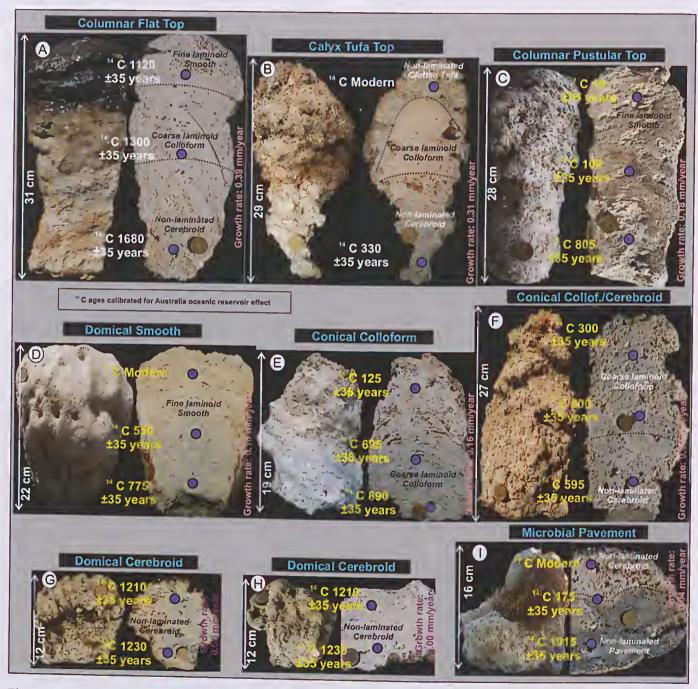


Figure 17 Microbial buildup slices showing internal fabrics, the sampling points and calibrated ¹⁴C ages with growth rates. (A) Columnar flat top structure with an internal shallowing-upward carbonate sequence represented by a basal non-laminated fabric passing upward to coarse laminoid and to fine laminoid fabric. (B) Calyx head with ornamented non-laminated fabric at top. (C) Columnar head with internal fine laminoid fabric and colonised by pustular at surface. (D) Domical structure with smooth top and internal fine laminoid fabric. (E) Conical colloform structure with a coarse laminoid internal fabric. (F) Conical structure with non-laminated fabric at base passing upward to a coarse laminoid fabric, (G, H) Domical cerebroid structure with internal non-laminated fabric. (I) Microbial pavement with a non-laminated fabric passing upward to a cerebroid morphology. (Jahnert & Collins 2012 figure 12).

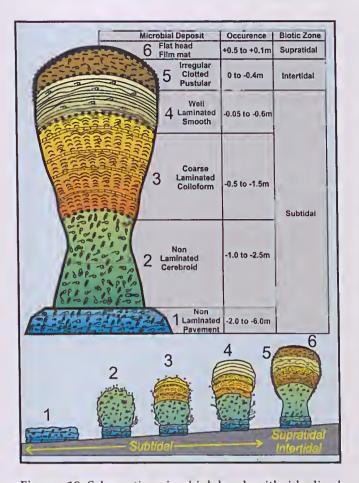


Figure 18 Schematic microbial head with idealised sequence of internal fabrics and their relative water depths. The structures often display a vertical sequence of internal fabrics in shallowing-upward arrangement or show truncated fabric sequences depending on environmental setting and timing of growth history. (Jahnert & Collins 2012 figure 17).

shallowing-upward carbonate system that commenced deposition in waters deeper than 1 m (e.g. see the sample labelled 'columnar flat top' in Figure 17) and support the late Holocene sea level fall inferred from other sea level proxies in Shark Bay.

Some microbial columnar forms exposed today in the supratidal zone consist internally of distinct fabrics that are non-laminated at the base (cerebroid) followed by coarse laminated (colloform), well-laminated (smooth) and a flat eroded top with a dark film veneer, representing a shallowing-up carbonate cycle (Figure 18). This is testimony to the process of sea level fall during the last 6000 years BP (Collins *et al.* 2006), which progressively stranded supratidal microbial deposits, providing an opportunity to study fabrics changing according to water level

Microbialite depositional model

Based on the improved knowledge of the nature and distribution of Shark Bay microbial deposits a revised facies model has been constructed (Figure 19). The last 2000 years are characterised by relatively extensive and prolific activity of microbial communities producing microbialites that are exposed in the supratidal zone and currently undergoing erosion, and intertidal forms. Microbialites are progressively colonising the subtidal zone as a consequence of sea level fall of about 2 m during the last 6000 years. Of particular importance is the significant increase of the known area of subtidal microbial habitat revealed in the mapping and reflected in the idealised cross-section which encapsulates the revised model

DISCUSSION

Tidal flats

The exceptional variety of microbial communities with their specific internal fabrics and their pattern of distribution according to topography and tidal zones identifies Shark Bay as a unique environmental setting.

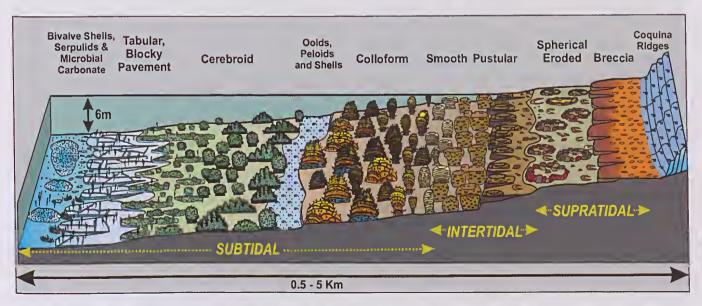


Figure 19 Shark Bay/Hamelin Pool facies model with extensive subtidal deposits. Note the exposed and now eroding supratidal microbial carbonates stranded by sea level fall. (Jahnert & Collins 2011 figure 4).

The modern microbial system is producing internal fabrics with stromatolitic, thrombolitic and cryptomicrobial characteristics laterally arranged within the same environment. Thrombolitic fabrics also occur in shallow intertidal environments with stromatolitic fabrics, in contrast to statements by other authors (Aitken 1967; Kennard & James 1986; Feldman & McKenzie 1998). The widespread nature and distribution of microbialites emphasises the applicability of Shark Bay as an analogue for ancient systems and increases scientific understanding of microbial deposits, which have significance as peritidal environmental markers and reservoir analogues. Table 1 is a summary of the contrasting properties of microbial mats and sediments of the three tidal flats studied.

The main shallow intertidal microbial mat in the tidal flats is the pustular mat which is characterised by a superficial vertical growth style (Golubic 1976a, b) of small mucilaginous pustules that also trap peloidal carbonate particles. After desiccation, this mat produces a mesoclotted fabric that may be designated thrombolitic (Logan et al. 1974b). In SEM images, pustular fabric exhibits two types of micrite: (i) a light pink to gold micrite that is apparently a product of mucilage mineralisation from communities of coccoid bacteria (Gloeocapsa, Chroococcus and Entophysalis), peloid fusion and EPS mineralisation; and (ii) a dark green to black micrite that surrounds grains and is pervasive, occurring as the last generation product of extensive microbial EPS biomineralisation, which is preferentially conducted below the sediment surface, mainly by communities such as sulfate-reducing bacteria and anoxygenic phototrophs (Decho 2000; Reid et al. 2000; Dupraz & Visscher 2005; Visscher & Stolz 2005; Vasconcelos et al. 2006; Dupraz et al. 2009). Microbial sulfide oxidation to elemental sulfur has a positive effect on alkalinity shifting the pH to alkaline, favouring carbonate precipitation (Vasconcelos et al. 2006). The microbial pavement is a permanently subtidal microbial deposit that occurs in Nilemah embayment as flat substrate that is being lithified to form a bioclastic grainstone composed of Fragum, serpulids, micro-gastropods, foraminifera and algae. The mesofabric is nonlaminated cryptomicrobial (sensu Kennard & James 1986) with open voids and shelter porosity. The microfabric is particularly related to the presence of bioclastic fragments of bivalve shells and ooids that are being lithified by a spongy pervasive micrite (seen in SEM) presumably from sulfate-reducing coccoid bacteria and methanogenic activity.

Communities of dominant cyanobacteria living on the surface of microbial mats and structures indicate correlation of predominantly laminated fabrics (tufted and smooth mats) with filamentous bacterial activity (*Lyngbya, Phornidium, Schizothrix* and *Microcoleus*) while non-laminated fabrics relate to the presence of coccoid bacteria. Within the intertidal zone in the pustular domain coccoid bacteria (Families Entophysalidaceae, Microcystaceae and Chroococcaceae) occur as gelatinous colonies of spherical to sub-spherical cells exhibiting mainly light green-blue colours, cell diameters of 2–20 µm with predominance of sizes of <5 µm. Subtidal colloform structures, despite their weakly laminated fabric, reveal the dominance of coccoid bacteria (Families Chroococcaceae, Entophysalidaceae and

Synechococcaceae) which are usually in gelatinous spherical colonies with *Chroococcus turgidus* showing the largest diameters (15–25 μ m). Microbial pavement is represented by non-laminated cryptomicrobial fabric with superficial coccoid communities (Families Chroococcaceae and Entophysalidaceae).

A lithified pavement that is commonly found centimetres below the modern surface was described in the tidal flats of Shark Bay and corresponds to an old Holocene surface. This surface was dated at 568, 503 and 490 ± 43 ¹⁴C years (calibrated ages) and is presumably related to a small regional sea regression. The ages obtained correspond to a period between 1444 and 1521 AD that is referred to in the literature as dry in the Southern Hemisphere. Lake Malawi's water level (from 1570 to 1850 years AD) was about 120 m lower than during the previous three centuries (Johnson et al. 2001) and ice core studies showed that atmospheric circulation intensity increased in the Polar South Pacific and North Atlantic at the beginning (ca 1400 AD) of the most recent Holocene rapid climate change known as the Little Ice Age (Kreutz et al. 1977). Microbial tidal flats in the Shark Bay World Heritage region occupy a 'niche area' of hypersalinity and alkalinity in the Holocene. Whilst they have apparently thrived during the relative climate stability of the last 6000 years of slowly falling sea level, their future is more uncertain under the predicted climatic change scenarios. Shark Bay tidal flats are reaching a critical moment in their evolutionary history; microbial deposits are highly susceptible to salinity and/ or sea level changes. Rapid sea level rise could lead to environmental instability, increased sediment mobility, salinity fall and microbial decline. On the other hand, if sea level falls significantly, microbial survival may also be threatened. A total detachment from the open embayment could generate a shallow evaporitic peritidal environment, and evaporites could progressively restrict microbial and molluscan life, creating a 'sabkha' environment.

In contrast, ancient microbial system analogues of the Phanerozoic and earlier often persisted for long (more than tens of millions of years) periods in stable tectonoeustatic and climatic settings allowing thick (many tens of stacked tidal flat cycles) sequences to accumulate over large areas of entire sedimentary basins recorded as microbial rocks. Examples from the Middle Ordovician of the Canning Basin Nita and Goldwyer Formations, Western Australia (Karajas & Kernick 1984); Ordovician of the central Appalachian Basin, United States (Pope & Read 1998); Permo-Triassic of central European Basins, Zechstein-Buntsandstein Group (Paul & Peryt 2000) and Cretaceous of South America, Santos Basin pre-salt sequence (Formigli et al. 2009) reinforce the significant past distribution of these microbial deposits which frequently serve as hydrocarbon reservoirs and sometimes as source rocks.

Hamelin Pool

Microbial activity in Hamelin Pool prospers in response to the unusual environmental conditions in a partially barred basin with restricted water exchange, high evaporation and hypersalinity. The hypersaline environment ensures a restricted diversity of eukaryote species; however the presence of *Fragum erugatum* which adapted and proliferated early during the first stages of hypersalinity around 4000 years ago, guarantees a large supply of bioavailable carbonate. Whilst the ultimate source of carbonate is yet unknown the linkage between high microbial activity and coquina productivity was established by 2000 years ago, perhaps promoted by sea level fall, reduced storm intensity and water chemistry evolution enriched in calcium ions. Processes of shell abrasion, dissolution and activity of microbial bioturbation might also act as a source of calcium ions which progressively became enriched in the system as the area evolved as an appropriate place for prolific microbial deposits to develop. As observed in fabrics of the oldest microbial deposits (cerebroid and microbial pavement) bivalves were fundamental as a biomass supplier to microbial construction. The extensive colonisation of intertidal and subtidal areas (0 to -2.5 m) by microbial organisms produced changes in aqueous CO, partial pressure as a result of consumption during photosynthesis. Also the process of CO, degassing (Kerrick 2001) produced by splashing waves, converts the system into a more alkaline environment which facilitates carbonate organomineralisation (Read 1976). Water parameters measured continuously in the south of Hamelin Pool recorded falls in the dissolved oxygen content of about 50% during nights, perhaps due to oxygen consumption, emphasising the high amount of CO, consumed during the day by photosynthesis.

Microbial communities also affect conditions by attracting minor amounts of metals (iron, nickel, lithium, strontium, rubidium, molybdenum and lanthanum); these are enriched in microbial samples from Shark Bay, and this process could influence the microenvironment's O₂ partial pressure. Gerdes (2007) reported that the presence of iron in cyanobacterial filaments maintained the partial pressure of oxygen at reduced levels as bacteria used iron to react with oxygen and thereby stabilise excessive oxygen content. Ferric hydroxides also may function as a barrier protecting the cyanobacteria group from the influence of sulfide sourced from deeper anoxic layers (Stal 1994) and used to produce the variety of pigments responsible for the variable colours visible at the surface and within the fabrics of microbial origin.

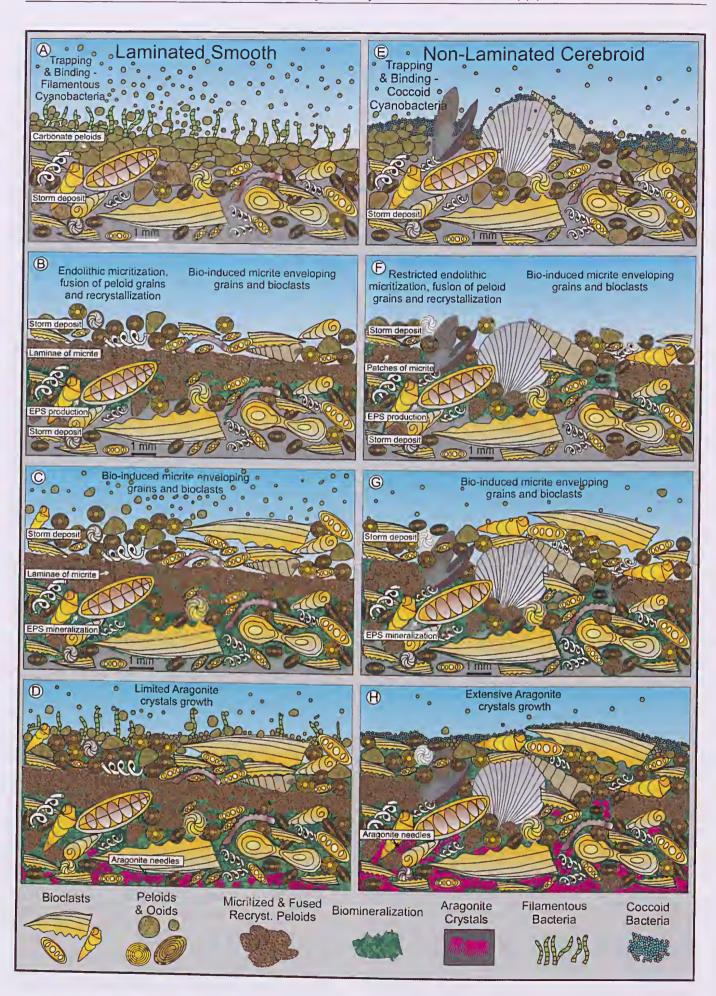
A summary of the stages producing laminated and non-laminated microbial fabrics is schematically represented in a sequence involving the stages highlighted by SEM and thin-section study (Figure 20). The constructional mechanisms of microbial heads depend on many factors and also on the presence and availability of coarse grains/bioclasts and fine carbonate particles and peloids. During storms coarse material is emplaced in the heads and after storms the deposition of peloids and fine carbonate particles predominates in shallower waters near smooth and colloform domains. Deeper portions are less well supplied by peloids and fine-grained carbonate particles. This is significant when considering microbial activity, which is deficient in micrite produced within fused peloids, and micrite patches are produced rather than laminated fabrics. A dark micrite that envelopes and connects grains and bioclasts, observed in thin-section and SEM (represented in green colour on the diagram in Figure 20) is responsible for a significant deeper water source of sediment stabilisation and is interpreted as a stage in structure construction which occurs presumably as a

result of sulfur-reducing bacterial activity (Riding 2000; Dupraz & Visscher 2005; Reid *et al.* 2000, 2003; Visscher & Stolz 2005; Baumgartner *et al.* 2006).

Microbial deposits in Shark Bay are notable not only because of their abundance and variable external morphologies but in view of the diverse microbial communities involved producing very distinctive internal fabrics. This study analysed a sequence of microbial deposits from shallow to deeper water seeking to advance the knowledge of the relationship between fabrics and water depth (Figure 18). Given the sea level regression in the last 2000 years of ~1.5 m, the fabrics were investigated with respect to what extent such variations are reflected in the resultant deposits. In the relatively small number of heads available for study few heads showed only one fabric type and it was clear that the fabrics often related to those formed in water depths >1 m, which are here termed non-laminated cryptomicrobial structures. They are complex with a significant amount of macroscopic eukaryotes responsible for bioturbation, disruption, skeletal framework and detritus accumulation. Within these fabrics, micrite occurs as bio-induced patches and disconnected clots distributed in coarse grainy sediment, resembling structures described as eukaryote stromatolites in the Bahamas (Feldmann & McKenzie 1998). The microbial structures of Hamelin Pool frequently display vertical sequences of internal fabrics revealing a shallowing-up sedimentary sequence, reflecting late Holocene sea level fall and emergence.

Aitken (1967 pp. 1164, 1171) defined thrombolites as 'non-laminated cryptalgal bodies characterised by a macroscopic clotted or spongy fabric... with microfabric consisting of centimetre-sized patches or clots of microcrystalline limestone (grain-size 8-20 microns) with rare clastic particles...'. Kennard & James (1986 pp. 494, 496) later introduced the term mesoclots as 'discrete colonies or growth forms of calcified, internally poorly differentiated, and coccoid-dominated microbial and also proposed the term communities' cryptomicrobial (a modification of cryptalgal from Aitken) fabrics for 'poorly differentiated, either mottled, patchy, or vague sediment fabrics that are attributable to constructional microbial activities, but that have been largely obscured by other organic and inorganic processes'.

Cerebroid structures and microbial pavement have a non-laminated fabric with micritic patches of mesoclots produced by coccoid bacteria. Also when examined in thin-section and SEM the fabrics reveal two micrite generations: a late micrite occurring as bio-induced micrite that envelopes grains and particles and one early micrite that occurs as patches of micrite resulting from peloid micritisation, fusion and recrystallisation (Jahnert & Collins 2012). Because of the absence of clear evidence of coccoid organomineralisation in the patches of micrite in cerebroid and microbial pavement internal fabrics, it was considered appropriate to describe the fabrics as 'cryptomicrobial non-laminated'. Following Shapiro (2000 p. 169) mesoclots are composed of a variety of microstructures including peloids, grumulous fabric, cement, and calcimicrobes...' and on that definition the deeper subtidal structures and fabrics of Shark Bay (bioinduced patches and disconnected clots; see above)



appear suitable to be termed thrombolites, but more investigation and sampling is needed to clarify the matter.

Although the microbial deposits in Shark Bay are referred to as stromatolites (Logan & Chase 1961; Logan et al. 1970; Davies 1970a; Playford 1972; Golubic 1973; Logan et al. 1974a; Hofmann 1976; Playford & Cockbain 1976; Reid et al. 2003 and many others), environmental changes, sea level variation and Bacteria/Archaea and diatoms in diversified communities may provide an explanation for the co-existence of, as reported here, stromatolites, thrombolites and cryptomicrobial deposits growing contemporaneously. Aitken (1967) considered thrombolites as a subtidal phenomenon and stromatolites as intertidal to supratidal deposits. Our investigations have revealed that pustular fabrics are shallow intertidal forms and their vertical growth style produces mesoclotted fabrics and thrombolites; subtidal occurrences have stromatolitic and cryptomicrobial fabrics.

Kennard & James (1986) and Feldmann & MacKenzie (1998) questioned the existence of modern carbonate systems with thrombolites arguing they share calcification with algae or have poorly defined clots which coalesce to form mesoscopic fabric different from the Paleozoic thrombolites. Pustular deposits in Shark Bay are producing mesoclots in an environment controlled by bacteria without any eukaryotic organisms sharing space. Also the modern thrombolite deposits of Lake Clifton and Lake Walyungup located south of Perth, Australia are constructed by classic mesoclots produced by filamentous cyanobacteria. These lacustrine thrombolites occur from shallow to deeper waters, displaying different external morphologies (Moore & Burne 1976), but with the same internal clotted thrombolitic fabric, providing an important example of modern thrombolite deposits.

Logan *et al.* (1974a) recognised that the interaction between microbial mats, sediments and processes of lithification and oxidation affect the deposits creating fenestral fabrics (porosity). Fenestral fabrics constitute an important element with applications in recognition and interpretation of ancient environments. Fenestral fabrics in Shark Bay are irregular within a bushy-like framestone in pustular deposits, a fine to medium subhorizontal laminoid fenestral fabric in smooth deposits and a coarse laminoid porous fabric in colloform deposits. We recognise that subtidal deeper deposits (cerebroid and microbial pavement) will produce an irregular fenestral fabric with voids between skeletal particles and bivalve shells and abundant shelter porosity. The effective

microbial influence and control in some of the subtidal deposits may be difficult to recognise when transformed to rocks because of lack of diagnostic fabrics and the amount of eukaryote skeletons. The presence of *Fragum erugatum*, serpulids, foraminifera, micro-gastropods, crustaceans, *Acetabularia*, Gigartinales, Fucales and bivalve borers living on subtidal buildups obstructs the normal growth of the heads producing irregular surfaces that may cause the head to split into branches, and also disturb and cause disruption of lamination. The peripheral growth of non-calcified algae however protects lower parts of heads from tidal current abrasion and erosion.

CONCLUSIONS

Tidal flats

This study has produced advances in the understanding of the Holocene microbial system and its establishment and development within three distinct tidal flats in Shark Bay (Jahnert & Collins 2013). It provides a new detailed characterisation of the taxonomic grouping of the dominant cyanobacterial consortium whilst describing previously undocumented tidal flat evolution, microbial colonisation and carbonate deposition.

A tentative chronological reconstruction of sea-level events emphasises the late Holocene microbial activity that produces carbonate deposits with distinct macro and microfabrics. These fabrics are related to the different microbial communities inhabiting very specific topographic tidal zones, and their products can be defined as stromatolitic to thrombolitic and cryptomicrobial sediments. Also recognised was the importance of the 'distal' subtidal zone microbial deposits at Nilemah (designated 'microbial pavement') extending to as deep as 6 m. These deposits provide an essential element to the system by consolidating the soft sandy or shelly substrate and thereby providing a hardground as a solid base for microbial head growth.

Environmental differences were recorded between tidal flat waters of different salinity and also in microbial sediments that possess, in permanent hypersaline waters (Nilemah), more positive δ¹³C and δ¹⁸O isotopic values and have an older ¹⁴C age. In Nilemah's permanently hypersaline domain, extensive subtidal microbial activity and colonisation generated structures (colloform) or spread as cryptomicrobial pavement. In the Garden Point and Rocky Point, tidal flats, where salinity values vary from metahaline to hypersaline, there is incipient colonisation of the subtidal substrate. Smooth mat is

Figure 20 Schematic sequence with the inferred mechanisms involved in the construction of microbial laminated smooth stromatolite (A–D) and non-laminated cryptomicrobial cerebroid (E–H) structures in Shark Bay. Microbial features have been exaggerated in scale for emphasis. In the smooth domain in upper subtidal conditions: (A) After storm activity and carbonate grains/bioclast emplacement, fine material in suspension is deposited creating a layer of peloidal grains with trapping and binding by filamentous microbes; (B) bioturbation, micritisation and fusion of peloids, creating lithified laminae of micrite after recrystallisation; (C) syndepositional processes of micrite generation which envelopes grains (green colour in diagram); (D) the last process is aragonite crystals growing in voids. The constructional process in deeper subtidal heads is; (E) after storms during a limited supply of peloids and over irregular surfaces of heads peloids accumulated in isolated patches, becoming bound by coccoid bacteria; (F) restricted activity of peloid fusion and micritisation; (G) extensive activity of grain/bioclast envelopment by micrite; (H) extensive growth of aragonite crystals filling void spaces. (Jahnert & Collins 2012 figure 16).

present but the subtidal zone does not display any microbial construction and is still receiving sandy influx from offshore (Garden Point) during storm events. In addition, these younger tidal flats are distinguished by seagrass growth at their sublittoral margins. There is also a large amount of quartz sand within the microbial fabrics because of the relatively late onset of microbial activity.

The following processes and findings are fundamental in explaining microbial prosperity in Shark Bay:

- (1) Falling sea-levels over the last 6000 years have been responsible for a shallowing in water depth in the embayments and tidal flats, causing a seaward shift of the depositional system. Because of the marine regression, new beach ridges have developed, mainly by longshore currents controlled by southerly winds and high tides in seaward zones. As a result, coastal reentrances have become protected by north–south-oriented barrier ridges, which restricted water circulation, generating extensive tidal flats exhibiting different stages of evolution and with different stages of microbial colonisation.
- (2) A shallowing-up sedimentary cycle was established for the Holocene deposits and correlated with sea-level variations, where microbial sediments aged younger than 2360 (1901 calibrated age) ¹⁴C years occupy the upper levels of the sedimentary column. The stressing conditions in the tidal environment were responsible for microbial establishment, trapping and binding or biologically inducing CaCO₃ precipitation, and producing laminated stromatolites (tufted, smooth and colloform), non-laminated clotted thrombolites (pustular) and cryptomicrobial non-laminated deposits (blister and pavement).
- (3) Tidal flats have low and smooth bottom gradients, varying from 20 to 80 cm/km at Garden Point and Rocky Point and from 20 to 150 cm/km in Nilemah. This low relief is responsible for the restricted tidal influx and well-defined tidal zonation. The intertidal zone occupies 70% of the environment with pustular mat dominance at Garden Point and Rocky Point. At Nilemah, the subtidal environment has significantly more widespread microbial deposits than the intertidal zone. Subtidal microbial deposits at Nilemah grow as mats (smooth) or microbial structures (colloform and microbial pavement) colonising submerged areas (0.5–6.0 m water depth) in the subtidal zone.
- (4) Microbial mats living in the supratidal and intertidal zones trap coarse carbonate and quartz grains and bioclastic fragments, in contrast to subtidal systems, which accumulate, after storms, a large amount of very fine to fine grains of carbonate peloids/ooids temporarily suspended by the high-water energy. Filamentous bacteria are the dominant group in the blister, tufted and smooth mats, and coccoid bacteria dominate the pustular, colloform and pavement structures. In the subtidal zone, colloform and microbial pavement structures coexist with other living organisms, such as serpulids, bivalves, diatoms, *Acetabularia*, crustaceans, algae, foraminifera and micro-gastropods, which are responsible for both exoskeleton supply and extensive bioturbation.
- (5) Microbial deposits are composed of carbonate grains and quartz, bioclasts, ooids, peloids,

microcrystalline micrite, organic matter and aragonite needles. Fabrics include laminated, sublaminar, scalloped, irregular, cryptomicrobial and clotted, depending on the amount of fine-grained carbonate and bioclasts available, bioturbation intensity, the microbial growth capacity and propensity to trap and bind or induce precipitation of CaCO₃.

(6) Relative age and degree of salinity elevation control the contrasting characteristics of the Garden Point–Rocky Point–Nilemah tidal-flat evolutionary sequence. Nilemah tidal flat exhibits the thickest and best-developed microbial system and was established before the other tidal flats, from 2360 years ago, with carbonate sediment composed mineralogically of aragonite with only traces of magnesium-calcite, calcite and gypsum, and revealing more positive values of δ^{18} C and δ^{18} O.

Hamelin Pool

Hamelin Pool is a shallow hypersaline environment with high microbial activity and diversity, and microbial carbonate deposition. The subtidal microbial structures and deposits are in fact, very extensive in the subtidal zone occupying 10 times the area of supratidal and intertidal deposits. More than 80% of microbial deposits occur in the subtidal zone and share space with eukaryotic organisms, especially Fragum erugatum. These have developed during the last few thousand years of stable hypersaline conditions and falling sea level. Microbial buildups prosper in water depths to a maximum of 2.5 m, constructing reef framework, although microbial influenced/induced deposits extend as semi-lithified surfaces and hardground to water depths of 6 m. These microbial tabular and blocky pavements occupy more than 220 km².

Subtidal structures are produced by aragonite through processes of trapping and binding particles (agglutination), micritisation, fusion and recrystallisation of peloids as well as presumed biologically-induced carbonate precipitation and lastly aragonite cement filling voids. Microbial structure morphologies consist of ellipsoidal, spherical, calyx, prismatic elongate, ridgelike, compound bladed and domical forms, reaching 1.5 m in height and depending on slope and wave energy or tidal movement, take on varied morphologies or produce widespread underwater pavements. Subtidal microbial structures have a microfabric complex of micritic composition containing ooids, peloids and bioclasts, with bivalves, serpulids, foraminifera, micro-gastropods and secondary quartz grains. Acetabularia, Gigartinales, Fucales and some living bivalves are external encrusters on microbial structures.

Subtidal deposits were recognised and mapped based on external organofacies, composition and morphologies as pustular, smooth, colloform, cerebroid, tabular or blocky pavement, bioclastic/peloidal sandflat, subtidal coquina, seagrass domain and bioclastic/ quartz sand. Subtidal structures have distinctive internal fabrics, with aragonitic micrite arranged in millimetric laminae or subspherical micrite patches which have different forms and fabrics such as well laminated (smooth), coarse laminoid (colloform), irregular clotted (pustular) and non-laminated cryptomicrobial (cerebroid and microbial pavement) producing microbial deposits with

stromatolitic fabric (smooth and colloform), thrombolitic fabric (pustular) and cryptomicrobial fabric (cerebroid and microbial pavement).

Finally, this study of microbial system morphogenesis in Hamelin Pool, Shark Bay has redefined the depositional model to include a new subtidal constructional microbial system. The findings emphasise the significance of a Holocene microbial system as one of the most important assets for the interpretation of ancient microbial deposits especially in view of the limited modern examples available to compare with the variety described from the rock record.

ACKNOWLEDGEMENTS

We are grateful to the Brazilian Oil Company Petrobras and Curtin University who sponsored this project. We appreciate the suggestions and collaboration of Pieter T Visscher during some of the field work activities. We also appreciate the support of the Department of Environment and Conservation scientists, particularly David Holley (Denham), Alan Kendrick (Kensington), for digital orthophotos, sampling permission and field support, as well as Landgate, Western Australia, for providing aerial-photos and orthophotos. We thank Fabio de Paula for field assistance. Cavalcanti and Damazio of the University of Rio de Janeiro are thanked for providing taxonomic identifications. We are grateful for the support of Brian and Mary Wake (Hamelin Station), Bob Morris and Shane Shulze (Hamelin Pool Caravan Park) and Rick, Alison and Samuel Fenny (Carbla Station). Analytical support was provided by several collaborating agencies who are also gratefully thanked. Alexandra Stevens assisted and is thanked for her contributions to refining the manuscript. Giada Bufarale provided untiring laboratory support. Gratitude is expressed to J Fred Read and Malcolm Walter for their comments and suggestions which have greatly improved earlier manuscripts.

REFERENCES

- Aitken J D 1967. Classification and environmental significance of cryptalgal limestones and dolomites with illustrations from the Cambrian and Ordovician of south-western Alberta. *Journal of Sedimentary Petrology* 37, 1163–1178.
- ALLEN M A, GOH F, BURNS B P & NEILAN B A 2009. Bacterial, archaeal and eukaryotic diversity of smooth and pustular microbial mat communities in the hypersaline lagoon of Shark Bay. *Goobiology* 7, 82–96.
- BAUMGARTNER L K, REID R P, DUPRAZ C, DECHO A W, BUCKLEY D H, SPEAR J R, PRZEKOP K M & VISSCHER P T 2006. Sulphate reducing bacteria in microbial mats: changing paradigms, new discoveries. Sedimentary Geology 185, 131–145.
- Berry P F & Playford P E 1997. Biology of modern Fragum erugatum (Mollusca, Bivalvia, Cardiidae) in relation to deposition of the Hamelin Coquina, Shark Bay, Western Australia. Marine & Freshwater Research 48, 415–420.
- Burne R V 1992. Lilliput's castles: stromatolites of Hamelin Pool Landscope 7, 34–40.
- Burne R V & James N P 1986. Subtidal origin of club-shaped stromatolites, Hamelin Pool. 12th International Sedimentological Congress, Canberra, Abstracts, p. 49.
- Burne R V & Johnson K 2012. Sea-level variation and the zonation of microbialites in Hamelin Pool, Shark Bay, Western Australia. Marine & Freshwater Research 63, 994–1004.

- Burne R V & Moore L S 1987. Microbialites: organosedimentary deposits of benthic microbial communities. *Palaios* 2, 241–254
- Burns B P, Goh F, Allen M & Neilan B A 2004. Microbial diversity of extant stromatolites in the hypersaline marine environment of Shark Bay, Australia. *Environmental Microbiology* 6, 1096–1101.
- BUTCHER B P, VAN DE GRAAFF W J E & HOCKING R M 1984. Shark Bay-Edel, Western Australia. Geological Survey of Western Australia 1:250 000 Geological Series Explanatory Notes.
- CAMPBELL S E 1982. The modern distribution and geological history of calcium carbonate boring microorganisms. *In*: Westbroek P & De Jong E W (eds) *Biomineralisation and biological metal accumulation*, pp. 99–104. D. Reidel, Dordrecht.
- CHIVAS A R, TORGENSEN H A & POLACH A 1990. Growth rates and Holocene development of stromatolites from Shark Bay, Western Australia. Australian Journal of Earth Sciences 37, 113–121.
- Collins L B, Zhao J X & Freeman H 2006. A high-precision record of mid-late Holocene sea-level events from emergent coral pavements in the Houtman Abrolhos Islands, southwest Australia. *Quaternary International* 145/146, 78–85.
- DAVIES G R 1970a. Carbonate bank sedimentation, eastern Shark Bay, Western Australia. In: Logan B W, Davies G R, Read J F & Cebulski D E (eds) Carbonate sedimentation and environments, Shark Bay, Western Australia, pp. 85–168. AAPG Memoir 13.
- DAVIES G R 1970b. Algal-laminated sediments, Gladstone Embayment, Shark Bay, Western Australia. In: Logan B W, Davies G R, Read J F & Cebulski D E (eds) Carbonate sedimentation and environments, Shark Bay, Western Australia, pp. 168–205. AAPG Memoir 13.
- Decilo A W 2000. Microbial biofilms in intertidal systems: an overview. Continental Shelf Research 20, 1257–1273.
- DUPRAZ C & VISSCHER P T 2005. Microbial lithification in marine stromatolites and hypersaline mats. *Trends in Microbiology* 13, 429–438.
- Dupraz C, Reid R P, Braissant O, Decho A W R, Norman S & Visscher P T 2009. Processes of carbonate precipitation in modern microbial mats. *Earth-Science Reviews* 96, 141–162.
- FELDMANN M & McKenzie J A 1998. Stromatolite—thrombolite associations in a modern environment, Lee Stocking Island, Bahamas. *Palaios* 13, 201–212.
- FORMIGLI J M F, PINTO A C C & DE ALMEIDA A S 2009. Santos Basin's pre-salt reservoirs development the way ahead. Offshore Technology Conference OTC 19953http://e-book.lib.sjtu.edu.cn/otc-2009/pdfs/otc19953.pdf>.
- Gerdes G 2007. Structures left by modern microbial mats in their host sediments. In: Schieber J, Bose P K, Eriksson P J, Banerjee S, Sarkar S, Altermann W & Catenau O (eds) Atlas of microbial features preserved within the clastic rock record, pp. 5–38. Elsevier, Amsterdam.
- GOH F, LEUKO S, ALLEN M A, BOWMAN J P, KAMEKURA M, NEILAN B A & BURNS B P 2006. *Halococcus liamelinensis* sp. nov., a novel halophilic archaeon isolated from stromatolites in Shark Bay, Australia. *Microbiology* 56, 1323–1329.
- Goii F Q Y 2007. Osmoadaptation mechanisms of cyanobacteria and archaea from the stromatolites of Hamelin Pool, Western Australia. PhD thesis, University of New South Wales, Sydney (unpubl.).
- GOLUBIC S 1973. The relationship between blue-green algae and carbonate deposits. *In*: Carr N G & Whitton B A (eds) *Biology of the blue-green algae*, pp. 434–472. Blackwell Scientific Publications, Oxford.
- GOLUBIC S 1976a. Organisms that build stromatolites. *In:* Walter M R (ed.) *Stromatolites* (*Developments in sedimentology* 20), pp. 114–126. Elsevier, Amsterdam.
- GOLUBIC S 1976b. Taxonomy of extant Stromatolite building Cyanophytes. In: Walter M R (ed.) Stromatolites (Developments in sedimentology 20), pp. 127–140. Elsevier, Amsterdam

- GOLUBIC S 1980. Early photosynthetic microorganisms and environmental evolution. *In*: Holmquist R (ed.) *Life Science and Space Research. COSPAR*, 18, pp. 101–107. Pergamon Press, Oxford.
- GOLUBIC S 1982. Stromatolites, fossil and recent: a case history. The modern distribution and geological history of calcium carbonate boring microorganisms. *Iu*: Westbroek P & De Jong E W (eds) *Biomiueralisation and biological metal accumulation*, pp. 313-326. D. Reidel, Dordrecht.
- Golubic S & Hofmann H J 1976. Comparison of Holocene and Mid-Precambrian Entophysalidaceae (Cyanophyta) in stromatolitic algal mats; cell division and degradation. *Journal of Paleontology* 50, 1074–1082.
- Grammer G M, Harris P M & EBERLI G P 2004. Overview and examples from the Bahamas. In: Grammer G M, Harris P M & Eberli G P (eds) Integration of outcrop and modern analogs in reservoir modeling, pp. 1–22. AAPG Memoir 80.
- HOCKING R M, MOORS H T & VAN DE GRAAFF W J E 1987. Geology of the Carnarvon Basin Western Australia. Geological Survey of Western Australia Bulletiu 133.
- HOFFMAN P 1976. Stromatolite morphogenesis in Shark Bay, Western Australia. *Iu:* Walter M R (ed.) *Stromatolites* (*Developments in sedimentology* 20), pp. 261–272. Elsevier, Amsterdam.
- JAHNERT R J & COLLINS L B 2011. Significance of subtidal microbial deposits in Shark Bay, Australia. Marine Geology 286, 106–111.
- Jahnert R J & Collins L B 2012. Characteristics, distribution and morphogenesis of subtidal microbial systems in Shark Bay, Australia. *Marine Geology* 303/306, 115–136.
- JAINERT R J & COLLINS L B 2013. Controls on microbial activity and tidal flat evolution in Shark Bay. Western Australia. Sedimentology 60, 1071–1099.
- Jahnert R J, De Paula O, Collins L B, Strobach E & Pevzner R 2012. Evolution of a coquina barrier in Shark Bay, Australia by GPR Imaging: architecture of a Holocene reservoir analog. Sedimentary Geology 281, 59–74.
- JOHN J 1993. Morphology and ultrastructure of the tubes of Mastogloia cocconeiformis (Bacillariophyta) from Shark Bay, Western Australia. Phycologia 32, 388–394.
- JOHNSON T C, BARRY S L, CHAN Y & WILKINSON P 2001. Decadal record of climate variability spanning the past 700 yr in the Southern Tropics of East Africa. Geology 29, 83–86.
- Karajas J & Kernick C N 1984. A prospective Nita Formation reservoir trend on the Broome Platform. *In*: Purcell P G (ed.) *The Canning Basin, W.A.*, pp. 169–177. Geological Society of Australia and Petroleum Exploration Society of Australia, Canning Basin Symposium, Perth.
- Kennard J M & James N P 1986. Thrombolites and stromatolites: two distinct types of microbial structures. *Palaios* 1, 492–503.
- Kerrick D M 2001. Present and past nonanthropogenic CO₂ degassing from the solid Earth. *Reviews of Geophysics* **39**, 565–585.
- Kreutz K J, Mayewski P A, Meeker L D, Twickler M S, Whitlow S I & Pittalwala 1 I 1977. Bipolar changes in atmospheric circulation during the Little Ice Age. *Science* 277, 1294–1296.
- LOGAN B W 1961. Cryptozoon and associate stromatolites from the Recent, Shark Bay, Western Australia. Journal of Geology 69, 517–533.
- Logan B W 1968. Western Australia In: Gill E D (ed.) Quaternary shoreline research in Australia and New Zealand, p. 110. Australian Journal of Science 31.
- Logan B W & Chase R L 1961. The stratigraphy of the Moora Group. Journal of the Royal Society of Western Australia 44, 14– 31.
- Logan B W & Cebulski D E 1970. Sedimentary environments of Shark Bay, Western Australia. *In:* Logan B W, Davies G R, Read J F & Cebulski D E (eds) *Carbonate sedimentation and environments, Shark Bay, Western Australia,* pp. 1–37. AAPG Memoir 13.

- LOGAN B W, DAVIES G R, READ J F & CEBULSKI D E 1970. Carbonate sedimentation and environments, Shark Bay, Western Australia. AAPG Memoir 13.
- LOGAN B W, HOFFMAN P & GEBELEIN C D 1974a. Algal mats, cryptalgal fabrics, and structures, Hamelin Pool, Western Australia. In: Logan B W, Read J F, Haga G M, Hoffman P, Brown R G, Woods P J & Gebelein C D (eds) Evolution and diagenesis of Quaternary carbonate sequences, Shark Bay, Western Australia, pp. 140–194. AAPG Memoir 22.
- LOGAN B W, READ J F, HAGA G M, HOFFMAN P, BROWN R G, WOODS P J & GEBELEIN C D 1974b. Evolution and diagenesis of Quaternary carbonate sequences, Shark Bay, Western Australia. AAPG Memoir 22.
- MACINTYRE I G, PRUFERT-BEBOUT L & REI P R. 2000. The role of endolithic cyanobacteria in the formation of lithified laminae in Bahamian stromatolites. *Sedimentology* 47, 915–921.
- Moore L S & Burne R V 1994. The modern thrombolites of Lake Clifton, Western Australia. *In*: Bertrand-Sarfati J & Monty C (eds) *Phanerozoic stromatolites II*, pp. 3–29. Springer, Netherlands.
- O'LEARY M J, HEARTY P J & McCullocii M T 2008. U-series evidence for widespread reef development in Shark Bay during the last interglacial. *Palaeogeography, Palaeoclimatology, Palaeoecology* 259, 424–435.
- Papineau D, Walker J J, Mojzsis S J & Pace N R 2005. Composition and structure of microbial communities from stromatolites of Hamelin Pool in Shark Bay, Western Australia. Applied and Environmental Microbiology 71, 4822–4832.
- Paul J & Peryt T M 2000. Kalkowsky's stromatolites revisited (Lower Triassic Buntsandstein, Hartz Mountains, Germany). Palaeogeography, Palaeoclimatology, Palaeoecology 161, 435–458.
- Pentecost A 1991. Calcification processes in algae and cyanobacteria. *In*: Riding R (ed.) *Calcareous algae and stromatolites*, pp. 1–19. Springer-Verlag, Berlin.
- Playford P E 1972. Algal stromatolites in the Devonian of the Canning Basin, Western Australia. *Annales de la Societe geologique de Belgique* 95, 401–402.
- PLAYFORD P E 1979. Stromatolite research in Western Australia. Journal of the Royal Society of Western Australia 62, 13–20.
- Playford P E 1990. Geology of the Shark Bay area, Western Australia. In: Berry P F, Bradshaw S D & Wilson B R (eds) Research in Shark Bay. Report of the France-Australe Biceutenary Expedition Committee, pp. 13–31. Western Australian Museum, Perth.
- PLAYFORD P E & COCKBAIN A E 1976. Modern algal stromatolites at Hamelin Pool, a hypersaline barred basin in Shark Bay, Western Australia. *In:* Walter M R (ed.) *Stromatolites* (*Developments in sedimentology* 20), pp. 389–411. Elsevier, Amsterdam,
- PLAYFORD P E, COCKBAIN A E, BERRY P F, ROBERTS A P, HAINES P W & BROOKE B P 2013. The Geology of Shark Bay. Geological Survey of Western Australia Bulletiu 146.
- POPE M & READ J F 1998. Ordovician metre-scale cycles: implications for climate and eustatic fluctuations in the central Appalachians during a global greenhouse, non-glacial to glacial transition. *Palaeogeography, Palaeoclimatology, Palaeoecology* 138, 27–42.
- Read J F 1976. Calcretes and their distinction from stromatolites.

 In: Walter M R (ed.) Stromatolites (Developments in Sedimentology 20), pp. 55–71. Elsevier, Amsterdam.
- Reid R P, James N P, Macintyre I G, Dupraz C P & Burne R V 2003. Shark Bay stromatolites: microfabrics and reinterpretation of origins. Facies 49, 299–324.
- Reid R P, Visscher P T, Decho A W, Stolz J F, Beboutk B M, Dupraz C, Macintyre I G, Paerl H W, Pinckne J, Prufert-Beboutk L, Steppe T F & Desmaraisk D J 2000. The role of microbes in accretion, lamination and early lithification of modern marine stromatolites. *Nature* 406, 989–992.

- RIDING R 1991. Classification of microbial carbonate. *In*: Riding R (ed.) *Calcareous algae and stromatolites*, pp. 21–51. Springer-Verlag, Berlin.
- RIDING R 2000. Microbial carbonates: the geologic record of calcified bacterial-algal mats and biofilms. *Sedimentology* 47, 179-214.
- STAL L G 1994. Microbial mats: ecophysiological interactions related to biogenic sediment stabilisation. *In*: Krumbein W G, Paterson D M & Stal L G (eds) *Biostabilisation of sediments*, pp. 41–53. University of Oldenburg, Oldenburg.
- Shapiro R S 2000. A comment on the systematic confusion of thrombolites. *Palaios* 15, 166–169.
- VAN DE GRAAFF W J E, HOCKING R M & BUTCHER B P 1983, Yaringa, Western Australia. Geological Survey of Western Australia 1:250 000 Geological Series Explanatory Notes.

- VASCONCELOS C, WARTHMANN R, MCKENZIE J, VISSCHER P T, BITTERMANN A G & VAN LITH Y, 2006. Lithifying microbial mats in Lagoa Vermelha, Brazil: modern Precambrian relics? Sedimentary Geology 185, 175–183.
- VISSCHER P T, REID R P & BEBOUT B M 2000. Microscale observations of sulphate reduction: correlation of microbial activity with lithified micritic laminae in modern marine stromatolites. *Geology* 28, 919–922.
- VISSCHER P T & STOLZ J F 2005. Microbial mats as bioreactors: populations, processes and products. *Palaeogeography*, *Palaeoclimatology*, *Palaeoecology* **219**, 87–100.
- Walter M R 1999. The search of life on Mars. Allen & Unwin, St Leonards.

Received 9 July 2013; accepted 25 February 2014



Drought and flooding rains: Western Australian water resources at the start of the 21st Century

DP COMMANDER

School of Earth and Environment, University of Western Australia, 35 Stirling Highway, Crawley, WA 6009, Australia philip.commander@bigpond.com

The drying climate of southwestern Western Australia has led to much reduced runoff and groundwater recharge, with consequent decline in groundwater levels affecting wetlands and groundwater-dependent ecosystems. Water level decline in the Gnangara Mound has been exacerbated by maturing pine plantations and groundwater pumping for public supply and horticulture, while desalination has replaced the failing surface water supplies from hills catchments. At the same time, the north and northwest of the State have an increasingly wet climate in the last decade. The challenge for the State is to optimise use of the existing water resources and make best use of the undeveloped surface and groundwater. With groundwater and surface water resources increasingly fully developed, the emphasis for the future will be on recycling and water-use efficiency.

KEYWORDS: climate variability, drought, groundwater, surface water, water resources.

INTRODUCTION

Drought and flooding rains characterise our climate, but Western Australia is experiencing prolonged drying in the southwest and contrary wetting in the north simultaneously. Water is often quoted as a limiting factor in the development of Western Australia: the State lacks major perennial rivers; rivers in the southwest are saline in those areas where their catchments extend into farmland; and much of the interior is characterised by salt lakes. Pronounced long dry seasons in the southwest and the north exacerbate the feeling of a waterless terrain and, apart from the wetlands on the Swan Coastal Plain, the presence of groundwater is rarely evident.

Settlement and development of Western Australia has been largely achieved using groundwater; there are few areas where stock water cannot be sourced, and the mining industry has adapted to use saline water. Only the Eastern Goldfields and Wheatbelt require water to be piped in from a significant distance. Dams in the Ord and the southwest, and the Gascoyne River, together with the Perth Basin's groundwater have sustained irrigated agriculture.

Water has always been high profile in the public consciousness. Perth is a groundwater-based city where many householders have their own bores and the aquifers are household names, while the symbol of rural Australia is the windmill (windpump).

The last decade has seen low rainfall and the near collapse of Perth's surface water catchments, the stalled development of the Yarragadee aquifer in the southwest, and in 2013, desalination accounts for about half of the Integrated Water Supply Scheme supplying Perth and much of the Wheatbelt and Goldfields. Climate change in the southwest has reduced the yield from surface water and strained the capacity of groundwater, especially at

the time licensed groundwater use in many areas has reached allowable limits. Climate change is a topical subject, yet there has only been relatively recent recognition of the contribution of rainfall cycles to the current climate.

A hundred years ago, the southwest was about to enter a 60 year period of above-average rainfall. The environment we see today is a mismatch of vegetation grown up in the high rainfall of 1920–1974, but maturing in a low rainfall period since 1975. Perth's water supply has moved through eras of natural springs, dug wells, artesian bores, dams, protection of catchments, and is now entering an era of desalination and recycling. This has brought an inevitable cost increase, yet high-quality drinking water remains the cheapest bulk commodity, and is low priced by world standards.

Water security into the future is a major issue. Climate-change issues, managing groundwater abstraction rates, and the present-day drying trend in the populous southwest corner of the State, all present major challenges. Western Australia has the fastest growing population of any Australian State and more people inevitably leads to more water usage. Western Australians already consume more water per head for all purposes than other Australian States and the State's groundwater resources have borne the brunt of this increasing demand.

The last decade has seen a national focus on water, stimulated by the Millennium Drought of 1998–2009, with the formation of the National Water Commission and its National Water Initiative, the National Centre for Groundwater Research and Training, CSIRO's Water for a Healthy Country Flagship, the Western Australia Department of Water, the Water For Food program in the Department of Agriculture and Food, and the four year initiative of the Department of Regional Development and Lands to assess, plan and investigate regional water availability under the Royalties for Regions program.

WATER MYTHS

The Western Australian population holds some very entrenched views regarding water and water supply. In the late 1890s, myths surrounded 'artesian' water-the magic of free-flowing water, in an age without ready access to power and pumps. The Western Australian Government, in 1896, embarked on diamond drilling to 3000 feet (914 m) for artesian water in granite near Coolgardie (against the advice of its then Government Geologist H P Woodward). Newly appointed Government Geologist A G Maitland commented 'a prevailing notion in certain circles is that if a well is only carried deep enough, an abundant supply of artesian water is assured' (Maitland 1897 p. 26), and reporting on his visit to the drilling, rated the 'chances of success as so infinitesimally small that as to render it useless to proceed any further with the work' (Maitland 1897 p. 28).

With desalination of local saline groundwater in the Kalgoorlie Region consuming an increasingly unsustainable amount of wood to fire the condensers, it was Chief Engineer C Y O'Connor's bold scheme to pipe water from a reservoir in the Perth Hills to Kalgoorlie that settled the water supply problem. This feat has dominated the thinking of the population brought up on O'Connor's achievement, and led to a long-distance pipeline mentality.

Watering the desert is a great Australian dream, but Western Australia's unique myth is piping water to Perth from the Ord River. The prohibitive costs were recognised in the 1970s, but the idea was taken up again in earnest by Ernie Bridge, Member for the Kimberley and Minister for Water Resources in the early 1990s (Bridge 1991). The public revelation of the existence of the Yarragadee Aquifer below the Blackwood Plateau (an underground lake reported in 'The Australian') forced abandonment of the project, but Bridge's death at Easter 2013, still spawned a number of letters to 'The West Australian' supporting long-distance pipelines as a source for Perth.

'Bringing water from the north' surfaced again at the 2004 state election with the Fitzroy canal proposal, in spite of a complete lack of basic information about the supposed groundwater source. Among industry professionals, the joke is that these schemes would never get considered if the map was the other way up – it is easier to visualise water running downhill from north to south! Numerous studies (e.g. Department of Premier and Cabinet 2006) have shown the cost of bringing water from the north cannot compete with the energy cost of seawater desalination.

In May 2000 a press conference unleashed on incredulous reporters news of the 'discovery' of the Officer Basin – 'Mining company discovers basin the size of England with first bore' read one headline' – and showed a suggested pipeline to supply Perth (Commander 2000). As indicated in the Kalgoorlie Boulder Waterlink study from the year before (Water Corporation 1999), the Officer Basin had long been considered a brackish source, and the subsequent drilling did not alter the position.

Because hydrogeology is often not readily understood by the public, development of groundwater is surrounded by half truths. Erroneous claims that the forests and biodiversity of the southwest would be threatened by the development of the southwest Yarragadee Aquifer obscured the very real issue of the potential effect on the Blackwood River and its tributaries. The uncertainties of predicting aquifer performance prior to development have led to very conservative decisions: the shelving of the Water Corporation's southwest Yarragadee proposal, and of the Vasse Coal proposal. The Environmental Protection Authority made recommendations against the latter in May 2011, citing serious environmental risks to nearby aquifers.

Misleading newspaper reports are seldom corrected. The West Australian (18 Oct 2007 p. 16; 17 March 2008 p. 9), quoted a study from the University of New South Wales, overestimating the magnitude of subsidence caused by groundwater extraction in Perth by an order of magnitude (Featherstone *et al.* 2012), and raising the spectre of damage to infrastructure, such as railways running up hill. In fact, the subsidence due to removal of water from elastic storage in the confined aquifers below Perth has been measured as 50 mm (Jia *et al.* 2007; Featherstone *et al.* 2012), spread over a large area, and is not a serious problem. Nevertheless, there was no public retraction, so the public is left confused.

The belief in water divining, and the (usually) erroneous concept of underground streams brought from northern Europe, is still endemic in the population, but much effort has been put into educating the younger generation through groundwater programs, for instance the Children's Groundwater Festival at Whiteman Park.

The recycling and drinking of treated waste water seems to be regarded with abhorrence by Australians, used to using pristine water once then discarding it, but it is clear that perceptions will have to change. Elsewhere in the world, people have had no choice for a long time—Londoners, for instance, are brought up being told that their drinking water has already passed through seven people (though this is largely a myth too).

WATER RESOURCE ASSESSMENT

Assessment of water resources in Western Australia began a little over a hundred years ago (Aquaterra 2009) with temporary river gauging stations on the Helena and Canning Rivers, and a further nine stations on streams in the hills near Perth commissioned between 1908 and 1911. Some 19 stations were established in 1939-1940 on the principal rivers in the southwest of the State, and in the 1950s and 1960s, monitoring began in the Indian Ocean Division and Timor Sea Divisions. While the quality of these early records was sometimes poor and infrequent, they provide a starting point for measurement records, and emphasise the importance of collecting rainfall and stream flow data. A statewide stream gauging network is now in place including telemetered continuous water level and electric conductivity (a measure of salinity), providing real time data for flood prediction.

The broad features of the State's artesian basins were also known a hundred years ago (Maitland 1913, 1919) although systematic groundwater resource assessment did not begin until 1962 (Allen 1997a, b). After a short

hiatus, following the recommendations of the Auditor General (2003), the Department of Water's State Groundwater Investigation Program (SGIP) was reinstated in 2006 (Johnson et al. 2005), and groundwater investigation is currently proceeding in the Perth Basin, Pilbara and West Kimberley. Regional groundwater monitoring of some 2500 bores is largely concentrated in the Perth Basin, and very localised elsewhere, with an additional network of 1300 bores monitoring groundwater level rise in the agricultural areas (George et al. 2008). Both surface water and groundwater monitoring data are available online through the Department of Water website.

CLIMATE VARIABILITY AND CLIMATE CHANGE

Rainfall is the ultimate origin of our water resources, but only relatively recently has there been recognition of the dominance of cyclicity in rainfall patterns on groundwater levels. Unlike the northern hemisphere, where tree-ring records, and hence rainfall proxies, go back thousands of years, the record in Western Australia has not until recently been extended before 1876. A reconstructed winter rainfall record showing a cyclic pattern of around 50 years duration (Figure 1) has now been proposed from a 350 year tree-ring record in Callitris columellaris near Lake Tay (100 km northeast of Ravensthorpe) by Cullen & Grierson (2009), and work on speleothems in southwest caves is continuing (Treble et al. 2003, 2008, 2013). According to this tree-ring analysis, southwestern Australia may have been settled at one of the wettest times in the last 350 years.

An intriguing discovery is that the recent decline in rainfall in southwest Western Australia mirrors that of North China, which has also been declining substantially since the mid-1960s. Using observed rainfall datasets in China and Australia Li *et al.* (2012) examined the relationship between the decline of southwest rainfall in early winter (May–July) and the reduction of North China rainfall in late summer (July–September) during 1951–2008, and found that a significant link exists between these two rainfall series. They suggested that poleward shifts of the Southern Subtropical High Ridge and the Northern Subtropical High Ridge over longitudes 110° to 150°E instigated by warming seasurface temperatures in the tropical Indian–western Pacific may have partially contributed to the rainfall reduction in both regions.

This teleconnection between rainfall in the southwest of Western Australia and North China allows the use of China's long historical climate record to reconstruct the past climate in southwest Western Australia. Li *et al.* (2012) showed that the reconstructed wet and dry periods are consistent with those in the paleoclimate data from the south coast from tree rings and the speleothem record at Moondyne Cave, and consistent with historical accounts of drought and flood events in the 19th Century.

The historical record of floods in the Swan River gives information on rainfall before records began in 1875 (Bureau of Meteorology 1929). Bearing in mind that the Helena and Canning Rivers are now regulated, the accounts of flooding in Perth Water in the period 1830–1926 are quite beyond the experience of most Perth residents, and gauging shows a decline in flow peaks in the Avon since 1971 (Figure 2).

The worst floods seem to have been in 1830, 1847, 1862, 1872, 1917, 1926, 1945, 1955, 1963 and 1964 (Bekle & Gentilli 1993; Bureau of Meteorology 1929; Binnie & Partners 1985), with the three largest floods in 1862, 1872 and 1926. In 1862, three weeks of relentless heavy rain over the Swan–Avon catchment covered Perth, including

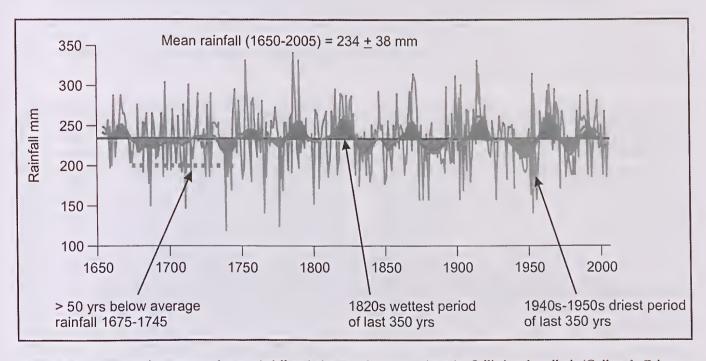


Figure 1 Reconstructed autumn-winter rainfall at Lake Tay from tree rings in *Callitris columellaris* (Cullen & Grierson 2009).

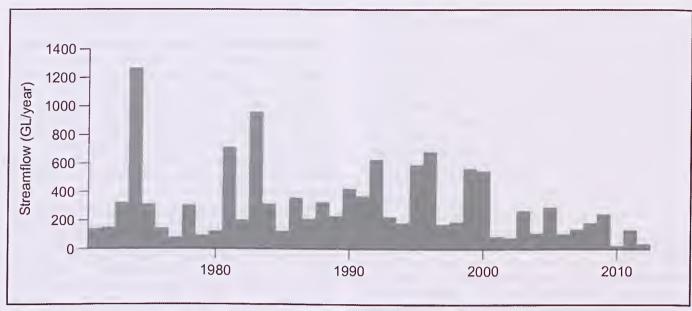


Figure 2 Annual streamflow in the Avon River at Walyunga station 616011 since 1971 (Department of Water).

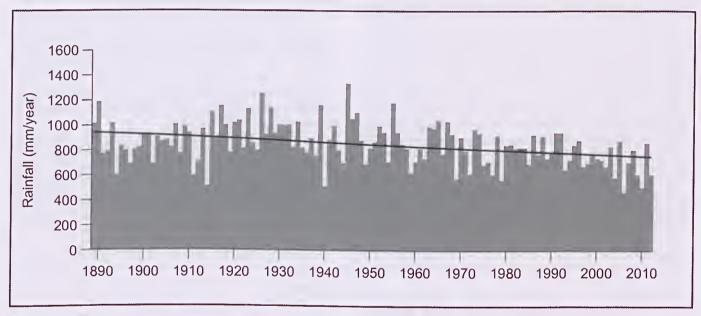


Figure 3 Perth annual rainfall 1889-2012.

the Causeway in over 2 m of flood waters for weeks. Properties and farms were destroyed and the bridge over Canning River was washed away. There were similar conditions in 1872.

In July 1926 severe and widespread flooding in the Avon, Swan and Helena River districts caused the Fremantle railway bridge and the Upper Swan bridge to collapse. The river burst its banks at Barrack Street, submerging jetties and bursting into offices. Flood waters encroached 137 m onto the foreshore. In South Perth, 14 houses were inundated between Scott Street and Mill Point. Waves surged along Mill Point Road and residents sailed a yacht up suburban streets, according to newspaper reports at the time. Market gardens along the river at Mounts Bay Road and in Belmont and Maylands were flooded by over a metre, and houses in South Guildford were submerged up to their roofs. Despite extensive reports of damage the waters did not reach the height of the 1862 floods.

Early maps of Perth show extensive wetlands, but by the late 1800s, there appear to be generally dry conditions. In the early 1900s though, rising groundwater levels were recorded from numerous locations including Lake Claremont (Butlers Swamp), Shenton Park Lake (Dysons Swamp), Mabel Talbot Reserve and Perry Lakes. It is difficult to separate the effects of clearing and rainfall but following high rainfall in 1917 and succeeding years (Figure 3), seasonal wetlands (previously named swamps) became permanent lakes. In the 1920s, drainage was a preoccupation in Perth, with the building of the tunnel outfall from Herdsman Lake and draining of Shenton Park Lake which had flooded adjacent houses. From historical evidence, Rich (2004) believed that Herdsman Lake experienced a unique period of higher water levels in 1920-1960 not experienced during 1847-1915, or after 1960. While the effects of clearing cannot be discounted as an additional factor, it appears our view of the

vegetation systems and groundwater-fed wetlands around Perth are coloured by a historically wet period.

By plotting the rainfall (Figure 4) expressed as Cumulative Departure from Mean (CDFM) Yesertener (2005, 2008) showed how the cyclic rainfall pattern controls shallow groundwater levels in the Gnangara Groundwater Mound, explaining the historical evidence from wetlands. Most recorded groundwater levels in the Gnangara Mound start in the early 1970s, and thus reflect the overall decline in response to the rainfall cycle.

SURFACE WATER RESOURCES

Darling Range runoff

Following the completion of the Victoria Reservoir in 1891, nearly all the suitable rivers in the Darling Range

have been dammed, but in the last decade, successive drought years (2001, 2006, 2010 and 2012) have severely impacted on streamflow (Figure 5). Streams which had flowed continuously from the 1960s ceased in the summer of 2011. It has been shown that evapotranspiration from deeply rooted eucalypts increases following drought years, lowering groundwater levels below streambed elevations, thereby reducing catchment water yield and dam inflows (Hughes *et al.* 2012). Rainfall that once generated significant flow during the winter months is now absorbed into dry soil horizons and more readily transpired.

The long-term groundwater and streamflow records, partly collected as a result of concerns about bauxite mining impacting on stream-water quality, have been invaluable in highlighting the interplay of vegetation, groundwater and streamflow in a drying climate with

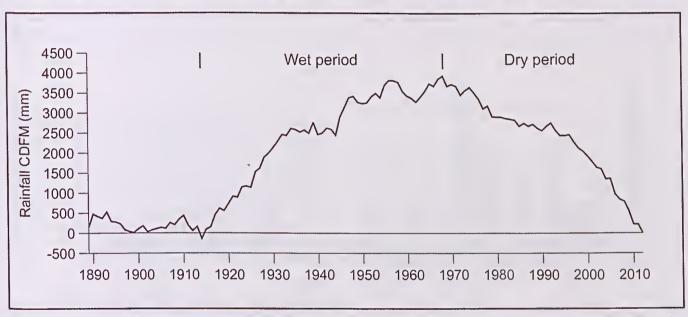


Figure 4 Perth rainfall plotted as cumulative departure from mean (CDFM). The period to 1913 is slightly below the long-term average. The period from 1917 to 1935 is well above and to 1969 somewhat above, whereas the period from 1975 is well below. Shallow groundwater levels mirror these trends.

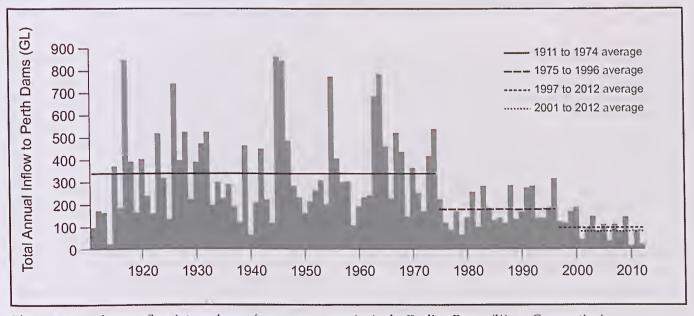


Figure 5 Annual streamflow into major surface water reservoirs in the Darling Range (Water Corporation).

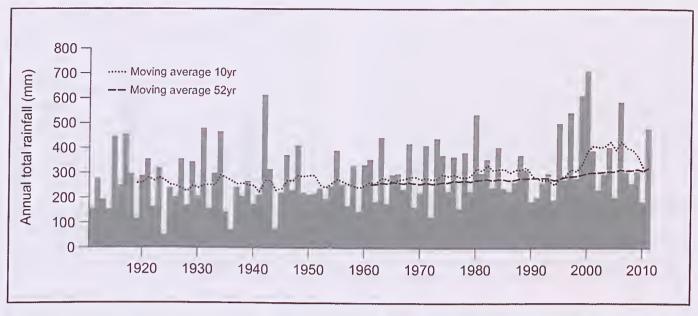


Figure 6 Averaged annual rainfall for the Pilbara for 1910–2012, along with backward moving averages of 10 and 52 years (Charles et al. 2013)

important implications for future water supply and the function of aquatic ecosystems.

Durrant (2009) reported on the difficulty of analysing trends in rainfall-runoff relationships since the stepchange in rainfall in 1975, which could not be attributed solely to the lower rainfall. Several factors affect individual catchments: increased surface-water and groundwater use, declining groundwater levels, land-use changes, farm dams and regulation. She noted that the rainfall analysis post-1975 showed a reduction in maximum daily rainfalls averaged over the last decade, which could impact on infiltration rates and general 'wetting up' of the catchment, resulting in a reduction of baseflow contribution to streams. These decreases in rainfall take time to reach equilibrium in the groundwater signature. Evidence of a change in the streamflow regime is seen with the shift in the peak flow month (one month later) that has been observed across all sites in the southwest.

Pilbara and Kimberley runoff

In contrast to the declining rainfall in the southwest, annual rainfall in Pilbara (Figure 6), and especially the central and east Pilbara has increased since about 1960 (Charles *et al.* 2013).

Systematic records of runoff in the Pilbara and Kimberley only commenced in the 1960s, though there is historical evidence from flood marks. The pattern of most northern rivers, both Pilbara and Kimberley, is one of increased runoff after 1999 (Figure 7). Devastating floods in the Gascoyne River at Carnarvon in 2010 and 2011 destroyed horticultural crops, cut off transport links and damaged homes and major infrastructure, and a new levee system is being built 10 km east of the town to mitigate the effect of flooding.

An unexpected feature of the increased runoff in the Pilbara was that of increases in groundwater salinity in bores adjacent to or recharged from rivers (Commander et al. 2004). This is possibly due to wetter catchments subject to evaporation, and denser vegetation close to the rivers, with the salts being recharged into groundwater with the first flush of succeeding runoff events. This effect has also been noted by Bennett & George (2011) in the Keep River, on the Northern Territory border. The river had been intermittent from 1965 until the initiation of the mid-1990s wet phase, becoming perennial (around 30 ML/day) in 2000, with a consequent increase in salinity from 100 mg/L to around 350 mg/L, forecast to increase to 1000 mg/L.

CLIMATE CHANGE EFFECT ON WATER RESOURCES

Surface water in the Darling Range

Silberstein et al. (2012) noted that the 16% rainfall reduction in the southwest after the mid-1970s resulted in declines of more than 50% in streamflows into the major water supply reservoirs in the Darling Range. They looked at projections from 15 global climate models (GCM) which suggest that the climate will be drier and hotter by 2030. Fourteen of the fifteen GCMs project further rainfall declines over the region, with a median decline of 8% resulting in a median decline in runoff of 25%, and continuing the downward trend in runoff. Projected runoff declines under a dry future scenario vary from 53% in the northern part of the Darling Range to 40% in the southern region. While proportional decline in runoff is greatest in the northern part of the area, the greatest volumetric declines are in the wetter basins in the southern part. The projections are also for a substantial reduction in the frequency of high runoff yielding years and a reduction in the area producing high levels of runoff. The results indicate the already large reductions in runoff recorded since 1975 are likely to continue under future climate projections.

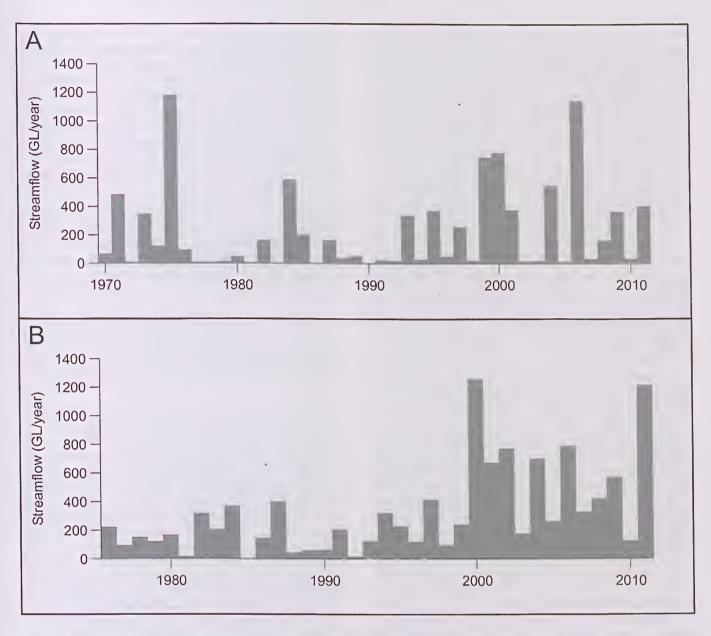


Figure 7 Annual streamflow in (a) Fortescue River at Gregory Gorge station 708002; (b) Dunham River at Dunham Gorge station 809321 (Department of Water).

Groundwater in the southern Perth Basin

Groundwater systems such as the Gnangara Mound have been shown to be very sensitive to rainfall changes (Yesertener 2005). Ali et al. (2012a) mapped out areas where groundwater levels may be most affected by a future drier climate and found that levels were most stable under areas with high water tables used for cleared dryland agriculture. McFarlane et al. (2012) concluded that in some cleared farming areas, groundwater levels would continue to rise, even under a dry climate scenario [the rate of groundwater level rise under farmland in the agricultural areas had slowed markedly since 2001, but are generally continuing (George et al. 2008)].

Ali et al. (2012b) assessed climate change impacts on water balance components of the regional unconfined aquifer systems in southwest coastal catchments. Compared with the historical period of 1975–2007,

reductions in the mean annual rainfall of between 15 and 18% are expected under a dry variant of the 2030 climate, which will reduce recharge rates by between 33 and 49% relative to that under the historical period climate. Relative to the historical climate, reductions of up to 50% in groundwater discharge to the ocean and drainage systems are also expected. They suggested that seawater intrusion is likely in the Peel–Harvey Area under the dry future climate and net leakage to confined systems is projected to decrease by up to 35% which will cause reduction in pressures in confined systems under current abstraction.

WATER RESOURCE MANAGEMENT

The current State Water Plan (Department of Premier and Cabinet 2007) followed the 2001 low-rainfall year, and its development period included the investigation and

shelving of the southwest Yarragadee proposal, the decision to build a seawater desalination plant, the Fitzroy canal proposal, the National Water Initiative, and the reconstitution of water management into the newly created Department of Water. The plan recognised the need to adapt to climate change, and the need for more metering and monitoring to improve the integrated management of water for the environment and other public values. It recognised that water use had tripled over 25 years, with groundwater accounting for over three-quarters of water used, and recognised that increasing demand for water would be met through water conservation, efficiency and recycling.

The plan outlined a water policy framework, among other things ensuring water management plans address issues in context of whole-of-State objectives, and facilitating the implementation of the National Water Initiative in a 'manner appropriate' for Western Australia. Where possible, planning was to be integrated to address the sustainability of the resource, water use, protection of catchments and drinking water sources and management of other impacts. One of the seven priority activities for 2007–2011 was to 'invest in science, innovation and education' specifically including 'groundwater investigation' (which had been previously addressed in the 2003 Auditor General's report).

The National Water Initiative was born out of issues affecting the Murray Darling Basin, but there are fundamental differences between the Murray Darling Basin and the variety of groundwater systems in Western Australia. Unlike the Murray Darling Basin, where groundwater and surface water resources are intimately connected, surface and groundwater in Western Australia are generally geographically separate, and the problem of double accounting, where the same water was allocated as both groundwater and surface water, does not generally apply in Western Australia. In an economic context, groundwater in Western Australia was already more often being used for high-value crops and the former Water Authority of Western Australia had

already been leading Australia in capping groundwater abstraction and defining environmental water provisions.

Full allocation, the amount the Department of Water is prepared to let licensed users pump, has now been reached in a number of groundwater sub-areas, and is likely to be reached throughout in the Perth Basin within a decade or so. Some areas are also over-allocated under the current drier climate, and programs have commenced to alleviate the situation. However, allocation limits are a management tool to control impacts, and questions such as 'how much water do we have?' or 'will it run out?' should really be reframed as 'at what rate are we prepared to use it, considering the impacts?' More intensive groundwater level monitoring and assessment of ecological dependencies are needed to assess whether impacts from groundwater abstraction are acceptable, and owing to the large groundwater storages, it may be many years before the effects of abstraction become apparent.

In the State's fractured rock provinces, where mining is by far the major user, it is not likely that usage will be severely restricted, given that mines are dispersed, though locally mines may wish to pump at rates exceeding a sustainable yield for a defined timeframe.

WATER RESOURCE DEVELOPMENT

Development of the State's water resources has risen rapidly in the last few decades (Figure 8). Much of the expansion in groundwater use has been in the Perth Basin for urban and irrigation supplies. Groundwater use shown in Figure 8 also includes hypersaline groundwater pumped in the goldfields for carbon-in-pulp processing of gold ores, saline and brackish groundwater used in nickel ore processing, and groundwater pumped to dewater mine pits. In the Pilbara, where most of the dewatering takes place, much of the water is fresh, and excess water not required for processing is mainly discharged to the environment, reinjected, or used for irrigation.

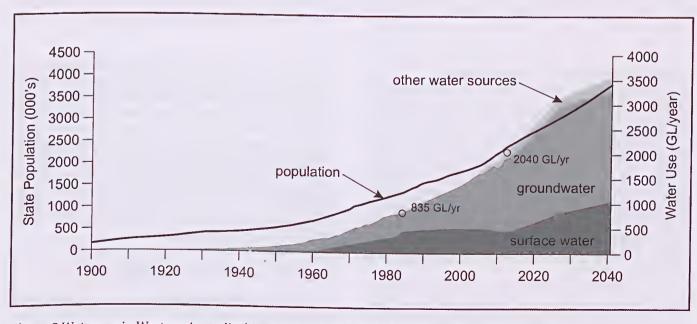


Figure 8 Water use in Western Australia, historical and projected to 2040 (Department of Water).

Irrigation

The current 'Water for Food' program of the Department of Agriculture and Food is aimed at stimulating irrigated agriculture in the Ord River Irrigation Area, Fitzroy Valley, La Grange (south of Broome), Pilbara, Carnarvon, West Midlands and Myalup. The project forecasts that about 1000 GL/a of low salinity (< 1000 mg/L TDS) water will be available to provide a base for 100 000 ha of irrigated agriculture. Some 7500 ha on the Weaber Plain, an area occupying a former channel of the Ord River extending across the Northern Territory border is currently being developed, following extensive investigation to assess the rising water table below the existing irrigation areas on the Ivanhoe and Packsaddle Plains, and to determine the suitability of the new land, which may require future groundwater pumping from the paleochannel aquifer. A program of land and water investigations commenced in 2012 across the sandplain soils surrounding Kununurra and the La Grange aquifer, and includes work with traditional owners coupled with an analysis of land tenure and markets for irrigated agricultural developments. Trials of cotton, and successful growing of melons, corn and cattle hay have demonstrated the potential of the La Grange area for irrigation.

Development of new crops has often proved difficult. In the Ord River Irrigation Area phases of development have included cotton, rice, sugar cane and sandalwood. In the northern Perth Basin, there has been recent expansion of vines, olives and almonds. Investigation of potential groundwater resources in the Birdrong Aquifer at Medo Station on the Wooramel River recently proved a resource of low salinity groundwater, but with poor recharge potential.

Mining

Development of the Goldfields was certainly hampered by lack of water in the first decade after 1892, leading to the abandonment of diggings, and the unsustainable use of wood-fired condensers to desalinate saline groundwater. The building of the Goldfields pipeline sufficed for the Kalgoorlie region until the 1980s when use of hypersaline groundwater from paleochannel aquifers enabled the current cycle of gold processing. Predictions made in the 1990s that groundwater from paleochannels in the Eastern Goldfields would run short, based on original estimates of groundwater storage, have not materialised, as paleochannel borefields have performed better than expected and yields have been maintained (Johnson 2007).

In the Pilbara, large-scale dewatering as mines go deeper below the water table has led to water surplus, and discharge of fresh groundwater to watercourses. Dewatering from the Woodie Woodie manganese mine is discharged to the Oakover River; from Yandi and Yandicoogina iron ore operations into Marillana Creek; and from Hope Downs iron ore mine to Weeli Wolli Creek. At the Marandoo iron ore mine, excess mine dewatering is being used to irrigate cattle fodder, rather than discharge it. Saline water at the Cloudbreak iron ore mine is re-injected into suitable aquifers. Potential iron mines in the Midwest are actively exploring for groundwater in the Murchison Catchment and the Permian sandstones in the eastern Carnarvon Basin.

Public water supply

Some 80 towns and numerous indigenous communities throughout the State depend on local groundwater supplies (Allen 1997b). In recent years, the supply from Geraldton's Allanooka borefield has been extended to Northampton and Yuna, replacing unsatisfactory local groundwater supplies, and groundwater from the Yarragadee Aquifer is being piped to Dunsborough, Margaret River and Bridgetown.

A significant water supply, discovered in the channel iron deposits of Bungaroo Creek, a tributary of the Robe River south of Pannawonica, is currently being pumped to Millstream for the West Pilbara Water Supply to be used in conjunction with the Harding Dam.

Garden bores

There are estimated to be about 170 000 garden bores in Perth, particularly located where blocks are large, the strata are sandy and the water table shallow, and less numerous in areas of clay, greater depth to water, hard limestone or high salinity. These are generally not licensed.

Lindsay (2004) assessed groundwater monitoring records in the urban area and concluded that in half of the 46 monitoring bores the water table had fallen an average of 0.8 m in 30 years. However, changes around the river and coast are small and greater changes occur inland. He concluded that water-level changes could be consistent with rainfall, though the bore network is not necessarily representative, with bores located preferentially near drains and wetlands. Smith *et al.* (2005) determined that groundwater levels had fallen under most of Perth in the previous 10 years period and that there was limited opportunity for additional backyard bores. Gaps in the bore monitoring record were identified, and have been subsequently filled using federal government funding.

The general fall in groundwater levels in many inner suburban areas has been tempered by urban infill, with increased infiltration via soakwells from greater roof and paving areas.

Superficial Aquifer

The Gnangara Groundwater System is the largest single groundwater source in Western Australia, servicing Perth's public water supply, parks and gardens, garden bores, horticulture and vineyards. Usage is around 321 GL/a (2009) close to one-fifth of Western Australia's groundwater use. It also supports wetlands, groundwater-dependent vegetation and stygofauna. The groundwater system encompasses the Superficial Aquifer (unconfined aquifer) between the Swan River and Gingin Book together with the underlying Leederville and Yarragadee Aquifers (the confined aquifers).

Of the total groundwater abstraction, 65% abstraction is from the Superficial Aquifer, of which 42% is for public water supply, 22% for horticulture, 18% for unlicensed garden bores and 9% for parks and gardens (Gallardo 2011).

The development of public supply borefields on the Gnangara Mound during the 1970s coincided with a major planting of pines and a decline in rainfall after 1975, and the combination of these three factors has resulted in declining water table levels of as much as 8 m, and consequent drying of wetlands. Ministerial conditions set for water levels around a number of wetlands in public wellfields in the 1990s have been breached, leading to 43 nearby production bores being turned off, though this measure has met with limited success.

A whole-of-government approach to managing the groundwater resources of the mound was set out in the Gnangara Sustainability Strategy. The Gnangara groundwater areas allocation plan (Department of Water 2009) sets out the approach to allocation and licensing for all water users on the Gnangara Mound. Through the plan, the Department of Water aims to achieve a reduction in the total abstraction from the Superficial Aquifer to address the trend of declining groundwater levels. The Forest Products Commission is responsible for modifying harvesting strategies of the pines to assist in increasing groundwater recharge, within the constraints of commitments to supply wood.

One of the management responses to declining groundwater levels on the Gnangara Mound has been the artificial maintenance of wetlands, using bores in either the superficial or underlying Leederville Aquifer. This has been attempted at Lake Jandabup, Lake Nowergup (Searle *et al.* 2011), Hyde Park and Perry Lakes and also, below the ground, in Yanchep Caves (Yesertener 2006), where seven of the estimated 300 caves previously had permanent groundwater-fed streams and pools supporting stygofauna associated with tuart root mat communities.

Lake Nowergup has been supplemented with groundwater from the Leederville Aquifer since 1989. With the continuing regional water table decline, supplementation has not been successful in meeting Ministerial water level criteria nor in maintaining a number of the lake's ecological values, including its

vegetation, though the slower rate of decline in lake levels has protected the lake from acidification and possibly from eutrophication. Seale *et al.* (2011) suggested it is unlikely that the current Ministerial conditions will be met by the continuation even of artificial maintenance, and recommended that the current criteria were no longer appropriate for the site.

Yarragadee and Leederville Aquifers

The Yarragadee Aquifer has been used in Perth since the early 1900s (Davidson 1995) and is now used almost exclusively for public water supply. Most of the 'independent artesian bores' were drilled at reservoir sites in the urban area so that the water could meet peak demand periods, the water not requiring treatment for iron, unlike the Leederville Aquifer. Expansion of use took place at the end of the 1990s with the Wanneroo and Pinjar borefields and three new bores in the Gwelup borefield (Scarborough, Carine and Gwelup). Figure 9 shows a typical response of water levels to the expansion in production. The drawdown cone in the Yarragadee now extends from Mandurah to beyond Gingin Brook (Figure 10).

Abstraction from the Yarragadee Aquifer exceeds natural recharge, therefore groundwater is being taken from storage (GHD et al. 2012), with induced recharge occurring in the 'recharge window' southwest of Gingin (Pigois 2009) where the Yarragadee Aquifer is directly overlain by the Superficial Aquifer. This is a relatively small area of around 30km² which gives rise to the lobe of low salinity groundwater in the Yarragadee Aquifer extending southwest to City Beach. The abstraction from the newer bores was intended to be a short-term measure, but the shortage of surface water supplies after 2001 has meant the bores have been continuously pumped.

The change in water levels in the Leederville Aquifer is similar, with induced recharge from the

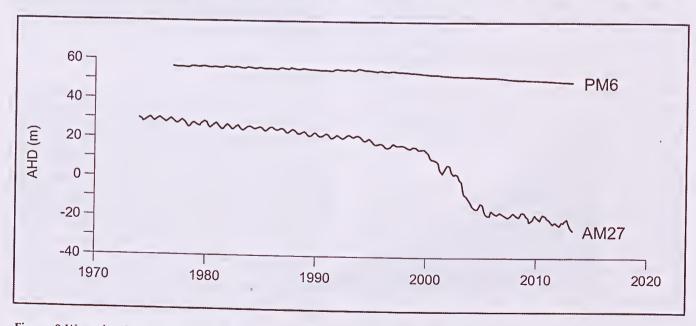


Figure 9 Water levels in the Superficial Aquifer at Pinjar Monitoring Bore PM6 on the central Gnangara Mound, and in the Yarragadee Aquifer Artesian Monitoring Bore AM 27 near Hillarys showing effect of increased production from confined aquifers in the late 1990s to early 2000s (Department of Water).

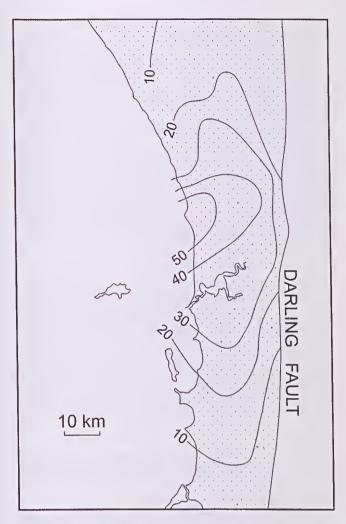


Figure 10 Change in water level (in metres) in Yarragadee Aquifer monitoring bores between 1977 and 2012 in the Perth region (Department of Water data). The Yarragadee Aquifer includes the Cattamarra Coal Measures adjacent to the Darling Fault in the southeast.

Superficial Aquifer indicated by the increased rate of water table decline near Leederville Aquifer production bores after increased pumping from the Leederville Aquifer (Figure 9).

Southwest Yarragadee case study

Exploration of the Yarragadee Aquifer in the southern Perth Basin started with the Quindalup Borehole Line in the 1960s. Subsequent drilling demonstrated greater thicknesses and lower salinity groundwater progressively to the south beneath the Blackwood Plateau. Following the low runoff in 2001 to the hills reservoirs, and lack of recovery to dam storage in the years after, the Water Corporation embarked on a comprehensive groundwater investigation involving some 12 000 m of drilling on the Blackwood Plateau with the aim of constructing a 45 GL/a scheme to augment the Integrated Water Supply Scheme. The difficulty of carrying out long-term pumping tests meant that there was a high degree of uncertainty about drawdown and effects on the Blackwood River and tributaries, supported by Yarragadee discharge, and the necessity of building a

full capacity scheme at the outset prevented a staged approach.

Public opposition from local water users, who had expectation the resources would be used for the benefit of local farming and industry, and from environmental groups (including 'Friends of the Yarragadee'), made the decision too political, and a second desalination plant was a more certain option. The end results are that it will be difficult in future to contemplate such a groundwater scheme, given the likely opposition; the management of the aquifer has become more conservative, and the public is left ill-informed about the effects of pumping (Commander 2009).

Geothermal use of aquifers

A number of geothermal exploration permits, with a view to power generation, have been taken up in the Perth Basin, but to date use of geothermal heat has been limited to heating swimming pools. The first use of hot groundwater in Perth is reputed to be at the Zoological Gardens bore (1898) to heat the reptile house. The Dalkeith 'hot spring' was used for bathing, though on an unregulated basis, and was closed when the Sunset Home bore (in the Yarragadee Aguifer) was capped in the 1950s. In the modern era, the Melville Pool bore (1996) was the first of a number of bores to be drilled specifically into the Yarragadee Aquifer for heating a swimming pool. By 2013 there were pairs of bores, a deep abstraction bore and a shallower reinjection bore, at nine installations (Melville, Christchurch, Claremont, Challenge, St Hilda's, Beatty Park, Cannington, Craigie and Hale). The St Hilda's project in Mosman Park is 1007 m deep and provides water at 49°C.

The most favourable sites for geothermal bores are in Perth's western suburbs where the Kings Park Formation is thick, providing a thermal insulator, resulting in higher temperatures in the underlying Yarragadee Aquifer. Groundwater is also being used for cooling the Pawsley Centre supercomputer in Kensington, in this case reinjecting heated water into the Mullaloo Sandstone at 100 m depth.

RESPONSES TO WATER SCARCITY IN THE SOUTHWEST

In the face of much reduced runoff into the hills reservoirs and the declining water levels on the Gnangara Mound, the Water Corporation has adopted a policy of 'Security through diversity' utilising a range of ways of closing the demand–supply gap: groundwater, surface water, desalination, efficiency and recycling, catchment management, and water trading. These measures have largely enabled the Integrated Water Supply Scheme to avoid the severe restrictions suffered by other state capitals, although Western Australia's situation is ongoing.

The decision to build Australia's first large-scale (45 GL/a) seawater desalination plant at Kwinana for public consumption followed the low rainfall in 2001, and the complications of carrying out the southwest Yarragadee investigation in a tight timeframe. Opening in 2006, the plant provided some 17% of the Metropolitan area's supply needs. Shortly after in 2007, the decision

was made to proceed with a second desalination plant at Binningup. This opened at the end of 2011, with a second stage opening in early 2013 giving an ultimate capacity of 100 GL/a, and contributing about half of the water supply to the Integrated Water Supply Scheme from desalinated seawater.

Groundwater desalination plants also exist elsewhere in the State, supplying the towns of Denham (from saline artesian water), Ravensthorpe, Hopetoun, Yalgoo and Rottnest (brackish shallow groundwater). Desalination plants supply water for mining across the State, and for industrial uses on the Burrup Peninsula.

An increasing emphasis on water use efficiency starting in the 1990s, has promoted the concept of water auditing—gaining an understanding of water use in industry and mining (Sturman *et al.* 2005). In 2001 the Water Corporation commenced a Water Wise Water Auditors Program which was tested in Kalgoorlie, where the capacity of the pipeline and storage at Kalgoorlie is limited. It involved such measures as replacing plumbing (eg dual-flush toilets and low-flow showerheads) and promoting brick paving over grass.

A \$6 million metering program on the Gnangara Mound to meter horticultural bores has also made growers more aware of their water use, and together with other measures has increased water use efficiency.

Promotion of garden bores in Perth, to reduce demand on scheme water, resulted in more drilling after the 2001 low rainfall year, and was encouraged by a subsidy scheme, and online publication of the Perth Groundwater Atlas, whereby landowners could easily calculate the depth to the water table on their property. A further incentive was the two-day-a-week roster for garden watering with scheme water, though later garden bores were subject to a three-day-a-week roster, to achieve equity and general water conservation. The Water Corporation has also run a 'Save 60' campaign aimed at reducing each person's use by 60 L per week. In the Metropolitan area, these measures have resulted in per capita scheme water consumption dropping by 30% in the last 10 years.

A greater awareness of the value of water has led to the concept of water sensitive urban design (Western Australian Planning Commission 2006, 2008; Department of Water 2013), making use of the geography and soils in Perth that are mostly favourable to recharge of stormwater, whether from roofs and paved areas, into soakwells, or road runoff into sumps and wetlands, which can then, fortuitously, be used by garden bores.

The move toward water use efficiency (recognised in the State Water Plan 2007) has extended to the Carnarvon Basin, where free-flowing artesian water had been discharged into 'bore drains' to water stock. It was estimated that 95% of the water was wasted, contributing to overgrazing and inability to control feral animals, and by the 1990s some 40 out of the 120 flowing bores drilled between 1910 and 1930 had ceased to flow. The Carnarvon Artesian Basin Rehabilitation Project was set up as voluntary program of capping and controlling the flowing bores, piping the water to troughs instead of open bore drains, with a subsidy of 80% cost to pastoralists. By 2003, 45 bores had been decommissioned, and a further 12 by 2007, saving 8 GL/a at the surface and an estimated 35 GL/a

in subsurface leakage, and allowing an overall rise in hydraulic head throughout the basin.

Treated waste water that is discharged to the ocean represents a significant resource. The Water Corporation has trialled Managed Aquifer Recharge from treated waste water at the Beenyup Waste Water Treatment Plant in Craigie, returning water to a high standard through microfiltration, ultraviolet radiation and a reverse-osmosis plant, prior to injection into the Leederville Aquifer, with intense monitoring and studies of the aquifer chemistry. The immediate benefit will be to raise hydraulic head in the aquifer, and it will be several decades before the injected water reaches nearby production bores. The decision to proceed with larger scale Managed Aquifer Recharge was made in August 2013.

Significant social consideration and education are required to increase water re-use for potable use, although reuse for non-potable use is already in place. The Kwinana Water Recycling Plant was commissioned in 2004 and processes about 24 ML/day of treated wastewater from the Woodman Point Waste Water Treatment Plant to produce high-quality, industrialgrade water for several local industries. The plant makes a significant contribution to the Water Corporation's 'climate resilience' target of achieving 30% wastewater re-use in the Perth metropolitan area by 2030. Importantly, it has significantly reduced industry demand in the area for scheme and bore water. In addition, all coastal waste water treatment plants that lack an ocean outfall (about 90%) dispose of their treated wastewater to a land site—often infiltration to the aguifer or a woodlot.

As the city's cheaper water sources have been developed, it is inevitable that costs of providing additional water will be progressively greater. The impact of higher cost desalination, and rebalancing fixed-consumption costs, has been felt by customers of the Integrated Water Supply Scheme with the base price of water per kL rising from around 50c per kL in 2007 to \$1.30 in 2013, with the top rate of \$2.60 per kL for household consumption over 550 kL/a. The sliding scale encourages lower water use, and reflects the cost of desalination compared with relatively cheap groundwater. Nevertheless, this is still inexpensive on a world comparison, and tap water is still a thousand times cheaper than bottled water.

While drinking water catchments have been maintained in a more or less pristine condition, to protect water quality, management of vegetation is being carried out to increase water flows. Pine tree removal on the Gnangara Mound should increase groundwater recharge, and thinning in hills catchments should increase runoff. However, a contrary program of revegetation in the Denmark catchment has been carried out to return the salinity to potable levels below 500 mg/L.

The increased awareness of the value of water is apparent in water trading. Commitments are made in the National Water Initiative to 'expand the trade in water'. This may be simple in a surface water system where sellers and buyers share the same water conduit, or can easily transfer water; it is not so straightforward for self-supply groundwater users with their own infrastructure

on their own property. Moreover, groundwater users are permitted to take water from a defined aquifer at a point where the effects of withdrawal are judged to be acceptable. Moving the point of withdrawal could have undesired effects, drawdown at wetlands, for instance, and therefore each trade needs to be separately assessed under the Rights in Water and Irrigation Act 1914. Skurray et al. (2013) identified the impediments to groundwater trading in the Superficial Aquifer on the Gnangara Mound and found that facilitating infrastructure was lacking, and price information unavailable. Moreover, limiting trading to within management areas, and overallocation and weak monitoring also impede the development of a market. Nonetheless, in terms of the National Water Initiative aim to 'bring about more productive water use' in the horticultural areas surrounding Perth, water is already used for high-value

Another National Water Initiative objective is effective water accounting, providing information on how much water there is, as well as information on who is using it and for what purposes. The Department of Water has commenced annual water accounting, trialling the Gnangara Mound. It is intended to report on changes in groundwater levels from year to year, rather than reporting on quantities. Average groundwater levels for the Gnangara Mound have already been reported since 1997, similar to reporting of reservoir storage levels.

ISSUES ASSOCIATED WITH GROUNDWATER ABSTRACTION

Appleyard & Cook (2009) found that acidification was taking place in the Mirrabooka Borefield, with aeration and oxidation due to the lowered watertable leading to low pH (typically <5 at the water table) and elevated concentrations of heavy metals. This is likely to be widespread over the Gnangara Mound, but is not apparent in deeper monitoring bores. A program of mapping acid sulfate soils has been carried out in the Murray River area of the Swan Coastal Plain, and on the Scott Coastal Plain, to identify areas which might be at risk of acidification owing to watertable decline.

Seawater intrusion is a potential issue for all coastal borefields in unconfined aquifers, affecting Esperance, Albany, Bunbury, Kwinana, Perth, Exmouth, Broome and Derby. Bores have already had to be abandoned in peninsula suburbs in Perth, and it is a potential issue in Perth's northern coastal suburbs. Kretchmer & Degans (2012) documented the inland movement of the seawater interface in the Superficial Aquifer as a result of pumping from the Water Corporation's north coastal scheme, though there is no evidence yet of increased salinity in production bores.

Production of groundwater from confined aquifers releases water from elastic storage, and is accompanied by a volume reduction as the aquifer matrix compacts. In Perth, subsidence had been too small to measure until the advent of highly accurate Global Positioning Systems (GPS), and large declines in hydraulic head. In 1996, a high resolution GPS, part of Geoscience Australia's Australia-wide network, was installed at the Hillarys tide gauge, and this registered the change in elevation due to

pumping the Yarragadee Aquifer (Figure 9). The total decline between 1996 and 2006 was about 50 mm (Jia *et al.* 2007; Featherstone *et al.* 2013), consistent with the head change of around 50 m in the Yarragadee (although the Leederville Aquifer also has an effect), and land subsidence over the Perth region can be inferred to mirror the change in head in the Yarragadee Aquifer (Figure 10).

Interest in shale and tight gas has caused concern among landowners worried about their groundwater supplies. Likely targets in the Perth Basin are the Kockatea Shale and Carynginia Formation several thousand metres deep, and below saline stagnant groundwater in overlying aquifers. The potential for fracking (hydraulic fracturing of shale and injecting sand and various chemicals) to affect the fresh groundwater flow systems in the overlying Yarragadee Aquifer is low, but a proliferation of deep wells crossing many strata increases the chances of a casing or grouting failure and leakage between aquifers. Nevertheless, various aquicludes separate the Kockatea Shale and Carynginia Formation from aquifers containing low-salinity groundwater.

Storage of carbon dioxide also has the potential to concern groundwater, mainly from the point of view of casing integrity, but there are unknown effects of pressurisation beyond natural levels. Current research on carbon capture and storage in aquifers is focussed on the Lesueur Sandstone on the Harvey Ridge west of Harvey. The Geological Survey of Western Australia drilled Harvey 1 in 2012 to depth of 2945 m where the aquifer is relatively shallow (Department of Mines and Petroleum 2012). Further evaluation and research is proceeding.

FUTURE FOR WATER RESOURCES

Increased demand for drinking water in the southwest is likely to be met by recycling and further desalination. Increased competition for horticultural water will see trading, higher prices and water use efficiencies. Pressure of urban development will continue to displace horticulture, and pressure will be placed on water catchments, when the cost of keeping the catchments pristine is weighed against the alternative costs of water treatment and seawater desalination.

In the north, the challenge for the State is to complete the irrigation developments in the Ord, develop groundwater in the Canning Basin, and use the untapped flows of the Fitzroy River, which have not been utilised since the failed Camballin irrigation project of the 1960s. While ever increasing quantities of water will be produced in the course of mining below the water table in the Pilbara, there is unlikely to be significant competition from or between mines as these are generally separated by considerable distances.

A drying climate is now built into water planning, and the era of low-cost surface water from hills' dams and groundwater is over, with desalination the new yardstick for price, and recycling the next opportunity, with public perception the greatest challenge.

Groundwater management has become more complex, with a need for more intense water-level monitoring and increasingly better understanding of hydrogeology as full

allocation is reached, and the effects of variable climate incorporated. Water managers face the challenge of managing a dynamic environment undergoing change due to a drying climate, and understanding what can and what cannot be protected.

While surface water resources and groundwater recharge have declined in the southwest, there still remains vast storage of groundwater in the Perth Basin, though the widespread effects of increased pumping the Yarragadee and Leederville Aquifers (originally for short-term drought relief) is now becoming apparent. Continuing groundwater investigation is needed to improve the monitoring network in the Perth Basin.

There still remain large areas of the State where the groundwater resource is poorly known. The Canning Basin, Western Australia's largest sedimentary basin, is inferred to contain large groundwater resources but only the extreme southwest and northwest coastal portions of the basin have been investigated. As one of the largest supposed shale gas resources in the world, access and need for water will stimulate groundwater investigation and use. The Officer Basin, the subject of much media attention in 2000, remains 99% unexplored, yet there are likely to be significant fresh or brackish water resources in the basin waiting to be discovered.

While some water information is becoming more accessible with the Bureau of Meteorology's responsibility to keep and disseminate data, other sources, for instance the vast treasury of consultants' reports that are held by Government, are not yet open file and the hydrogeological mapping program, which came to a halt, has not been replaced by public access to digital information. Reporting in the form of water accounting will bring a greater transparency, and as more information becomes available it will be ever more important to integrate and consolidate the public and private knowledge.

ACKNOWLEDGEMENTS

Don McFarlane, Richard George and Chris O'Boy made significant contributions to the paper and Jacqui Durrant and Simon Rogers assisted with provision of surface water information and figure preparation. Colin Branch and Roger Hocking suggested substantial improvements to the text. Craig Miskell drafted the figures.

REFERENCES

- ALI R, McFarlane D, Varma S, Dawes W, Emelyanova I & Hodgson G 2012b. Potential climate change impacts on the water balance of regional unconfined aquifer systems in south-western Australia. *Hydrological Earth Systems Science* 16, 4581–4601.
- ALI R, McFarlane D, Varna S, Dawes W, Emelyanova I, Hodgson G & Charles S 2012a. Potential climate change impacts on groundwater resources of south-western Australia. *Journal of Hydrology* 475, 456–472.
- ALLEN A D 1997a. A history of hydrogeology in the Geological Survey of Western Australia 1988–1995. Geological Survey of Western Australia Annual Review for 1995–96, 11–21.
- ALLEN A D 1997b. Groundwater: the strategic resource—a geological perspective of groundwater occurrence and importance in Western Australia. Geological Survey of Western Australia Report 50.

- Appleyard S & Cook T 2009. Reassessing the management of groundwater use from sandy aquifers: acidification and base cation depletion exacerbated by drought and groundwater withdrawal on the Gnangara Mound, Western Australia. *Hydrogeology Journal* 17, 579–588.
- AQUATERRA 2009. Strategic review of the surface monitoring network report. Report for Department of Water.
- Auditor General 2003. Second Public Sector Performance report 2003. Western Australia Auditor General Report 7.
- Bekle H & Gentilli J 1993. History of the Perth Lakes. *Early Days* 10, 442–460.
- Bennett D L & George R J 2011. Surface water characteristics of the Weaber Plain and lower Keep River Catchments: data review and preliminary results. Department of Agriculture and Food, Resource Management, Technical Report 370.
- BINNIE AND PARTNERS 1985. Avon River flood study. Report for Public Works Department, Western Australia.
- BRIDGE E 1991. The Great Australian Dream. Private publication of Minister for Water Resources, Western Australia.
- BUREAU OF METEREOROLOGY 1929. Results of rainfall observations made in Western Australia. Government Printer, Melbourne.
- CHARLES S P, Fu G, SILBERSTEIN R P, MPELASOKA F, McFARLANE D, HODGSON G, TENG J, GABROVSEK C, ALI R, BARRON O, ARYAL S K, DAWES W, VAN NEIL T & CHIEW F H S 2013. Interim report of the hydro climate of the Pilbara: past, present and future. A report to the Western Australia Government and industry partners from the CSIRO Pilbara Water Resources Assessment, CSIRO Water for a Healthy Country, Australia.
- COMMANDER D P 2000. Massive water find in the Officer Basin: Western Australian Geologist 396, 6–8.
- COMMANDER D P 2009. New water from old sources: case study of the south-west Yarragadee aquifer. *The Australian Geologist* 151, 20–22.
- COMMANDER D P, MARTIN M W & DOHERTY R 2004. Increasing groundwater salinity in north-west Australia a result of exceptionally wet years. In: Dogramaci S & Waterhouse A (eds) Engineering salinity solutions: 1st National Salinity Engineering Conference 2004. Barton, ACT, pp. 73–77. Engineers Australia, 2004
- Cullen L E & Grierson P F 2009. Multi-decadal scale variability in autumn-winter rainfall in south-western Australia since 1655 AD as reconstructed from tree rings of *Callitris columellaris*. Climate Dynamics 33, 433–444.
- DAVIDSON W A 1995. Hydrogeology and groundwater resources of the Perth region WA. *Geological Survey of Western Australia Bulletin* 142.
- Department of the Premier and Cabinet 2006. Options for bringing water to Perth from the Kimberley; an independent review, http://www.water.wa.gov.au/PublicationStore/first/64772.pdf>
- Department of the Premier and Cabinet 2007. State Water Plan 2007. http://www.water.wa.gov.au/PublicationStore/first/74923.pdf>
- DEPARTMENT OF MINES AND PETROLEUM 2012. South West CO₂ Geosequestration Hub; project and activity progress report for the Global Carbon Capture and Storage Institute. http://www.dmp.wa.gov.au/documents/South_West_Hub.pdf>.
- DEPARTMENT OF WATER 2009. Gnangara groundwater areas allocation plan. Department of Water Western Australia Water Resource Planning Series 30.
- Department of Water 2013. Water resource considerations when controlling groundwater levels in urban development. Department of Water Western Australia.
- Durrant J 2009. Streamflow trends in south west Western Australia. Department of Water Western Australia Surface Water Hydrology Series HY32.
- FEATHERSTONE W E, FILMER M S, PENNA N T, MORGAN L M & SCHENK A 2012. Anthropogenic land subsidence in the Perth Basin: challenges for its retrospective geodetic detection. *Journal of the Royal Society of Western Australia* 95, 53–62.

- Gallardo A 2011. Resource evaluation report Gnangara groundwater areas allocation plan. Department of Water Western Australia Hydrogeological Report Series HR 312.
- GEORGE R J, SPEED R J, SIMONS J A, SMITH R H, FERDOWSIAN R, RAPER G P & BENNETT D L 2008. Long term groundwater trends and their impact on the future extent of dryland salinity in WA in a variable climate. Proceedings of the 2nd International Salinity Forum, Adelaide 30 March-3 April 2008 (CD).
- GHD, ECOSEAL, VANESSA O'KEFFE & HAMSTEAD CONSULTING 2012. Guidance for groundwater storage utilisation in water planning. National Water Commission Canberra, Waterlines Report Series 81.
- Huches J D, Petrone K C & Silberstein R P 2012. Drought, groundwater storage and streamflow decline in southwestern Australia. *Geophysical Research Letters* 39, DOI: 10.1029/2011GL050797.
- JIA M, ENGLISH P, COMMANDER D P & JOHNSTON G 2007. GPS observation of compaction or expansion of the Perth Basin aquifer system. American Geophysical Union Fall Meeting 2007 Abstract G43B-1212.
- JOHNSON S L 2007. Groundwater abstraction and aquifer response in the Roe Palaeodrainage (1990 - 2001). Department of Water Western Australia Hydrogeological Record HG23.
- Johnson S L, Commander D P, O'Boy C A & Lindsay R P 2005. Proposed groundwater investigation program in Western Australia (2005 to 2020). Department of Environment Western Australia Hydrogeology Record HG 10.
- Kretschmer P & Degans B 2012. Review of available groundwater in the Superficial aquifer for the Yanchep, Eglinton and Quinns groundwater subareas. Department of Water Western Australia Hydrogeological Report HR330.
- LINDSAY R P 2004. Water level monitoring results for the superficial aquifer in the Perth Urban Area. Department of Environment Western Australia Hydrogeology Report HR 225.
- Li Y, Li J & FENG J 2012. A teleconnection between the reduction of rainfall in southwest Western Australia and North China. *Journal of Climate* 25, 8444–8461.
- MAITLAND A G 1897. Annual progress report of the Geological Survey for the year 1896. Department of Mines Western Australia.
- MAITLAND A G 1913. Appendix M. The artesian water resources of Western Australia. Report of Proceedings Interstate Conference on Artesian Water, Sydney, 1912.
- Maitland A G 1919. The artesian water resources of Western Australia. *Geological Survey of Western Australia Memoir* 1, Part II, Section 24, pp. 5–7.
- McFarlane D, Stone R, Martens S, Thomas J, Silberstein R, Ali R & Hodgson G 2012. Climate change impacts on water yields and demands in south-western Australia. *Journal of Hydrology* 475, 488–498.
- Pigois J-P 2009. Conceptual geology of the north Gnangara Mound. Department of Water Western Australia Hydrogeological Report HR 228.

- Rich J F 2004. Integrated mass, solute, isotopic and thermal balances of a coastal wetland. PhD thesis, Murdoch University, Murdoch (unpubl.).
- SEARLE J A, HAMMOND M J & BATHOLS G 2011. Perth Shallow Groundwater Systems Investigation: Lake Nowergup. Department of Water Western Australia Hydrogeological Record HG 40.
- SILBERSTEIN R, ARYAL S, DURRANT J, PEARCEY M, BRACCIA M, CHARLES S, BONIECKA L, HODGSON G, BARI M & McFARLANE D 2012. Climate change and runoff in south-western Australia. *Journal of Hydrology* 475, 441–455.
- Skurray J, Pandit R & Pannell D J 2013. Institutional impediments to groundwater trading: the case of the Gnangara groundwater system of Western Australia. *Journal of Environmental Planning and Management* 56, 1046–1072.
- SMITH A, POLLOCK D & McFarlane D 2005. Opportunity for additional self supply of groundwater from the superficial aquifer beneath Mctropolitan Perth. Client Report, CSIRO: Water for a Healthy Country National Research Flagship, Canberra.
- STURMAN J, Ho G & MATTHEW K. 2005. Water auditing and water conservation. IWA Publishing, London.
- TREBLE P C, BRADLEY C, WOOD A, BAKER A, JEX C N, FAIRCHILD I J, GAGAN M K, COWLEY J & AZCURRA C 2013. An isotopic and modelling study of flow paths and storage in Quaternary calcarenite, SW Australia: implications for speleothem paleoclimate records. *Quaternary Science Reviews* 64, 90–103.
- Treble P C, Fairchild I J & Fischer M J 2008. Understanding climate proxies in southwest-Australian speleothems. *PAGES News* **16**, 17–19.
- TREBLE P C, SHELLEY J M G & CHAPPELL J 2003. Comparison of high resolution sub-annual records of trace elements in a modern (1911-1992) speleothem with instrumental climate data from southwest Australia. *Earth and Planetary Science Letters* 216, 141–153.
- WATER CORPORATION 1999. Kalgoorlie Boulder WaterLink Final Report. Water Corporation Western Australia, Perth.
- Western Australian Planning Commission 2006. State planning policy 2.9: Water Resources. Western Australian Planning Commission, Perth.
- Western Australian Planning Commission 2008. Better urban water management. Western Australian Planning Commission. Perth.
- YESERTENER C 2005. Impacts of climate, land and water use on declining groundwater levels in the Gnangara Groundwater Mound, Perth, Australia. *Australiau Journal of Water Resources* 8, 143–152.
- YESERTENER C 2006. Assessment of the artificial maintenance of groundwater in Yanchep caves—groundwater flow modelling. Department of Water Western Australia Hydrogeological Record HG13.
- YESERTENER C 2008. Assessment of the declining groundwater levels in the Gnangara Groundwater Mound. Department of Water Western Australia Hydrogeological Record Series HG14.

Received 13 August 2013; accepted 14 February 2014



Some Australian contributions to meteoritics from the 19th to the 21st Centuries

AWR BEVAN

Department of Earth and Planetary Sciences, Western Australian Museum, Locked Bag 49, Welshpool DC, WA 6986, Australia.

Australia Museum. Locked Bag 49, Welshpool DC, WA 6986, Australia Australia Museum. Locked Bag 49, Welshpool DC, WA 6986, Australia

Meteorites are fragments of natural debris that survive their fall to Earth from space, and meteoritics is the science of their study. Meteorites are fundamental to our understanding of the origin and early evolution of the Solar System. Many have remained virtually unaltered for 4.56 Ga and represent some of the original materials from which the planets were constructed. From the 19th Century onwards contributions to the understanding of planetary materials have been made by Australian scientists in the fields of meteorite recovery, mineralogy, petrology and metallurgy of meteorites, meteorite classification, isotopic studies, geochronology, impact cratering and Solar System formation. This paper documents some of the significant achievements that have been made.

KEYWORDS: chondrites, geochronology, irons, isotopes, meteorites, mineralogy, petrology, stony-irons.

INTRODUCTION

Meteorites are a fundamental source of information on the origin and early evolution of the Solar System, and meteoritics is the science of their study. The majority of meteorites are fragments broken from asteroids in solar orbits between Mars and Jupiter, although few specific asteroids have been identified as possible sources. Other meteorites are fragments from the Moon and Mars. Many asteroidal meteorites have remained virtually unaltered for 4.56 Ga and provide evidence of the earliest formative processes of the Solar System, ranging from stellar evolution of the nearby galactic region, condensation and melting of early materials, nebula and preplanetary disk formation, and the accretion, differentiation and disruption of planetesimals and protoplanets.

While meteorites have been studied for over 300 years, with the successful NASA (Apollo) and Russian (Luna) sample recovery missions from the Moon from 1969 to 1976, the mid-20th Century saw a rapid expansion in planetary science world-wide. Significant contributions to our understanding of the early Solar System have been made by Australian scientists working both in Australia and overseas, and by overseas scientists working in Australia. This paper documents some of the significant discoveries that have been made from the recognition, recovery and study of planetary materials. In addition, the development of ever more sensitive and sophisticated analytical equipment through the 20th Century parallels the heightened interest in planetary materials, and was largely driven by it.

METEORITIC MATERIALS

Three main groups of meteorites are recognised, determined by the relative amounts of metallic Fe-Ni and ferromagnesian silicates they contain. Irons are composed almost entirely of metal; stones are made

predominantly of silicates (olivine, pyroxene and feldspar) similar to those occurring in terrestrial basalts, but may also contain appreciable amounts of metal; and stony-irons are mixtures of metal and silicates in roughly equal proportions. Stony meteorites are the most common, accounting for more than 95% of those observed to fall, whereas irons and stony-irons are rare, accounting for around 4% and 1% of the meteorite flux, respectively.

Two groups of stones are recognised; chondrites and achondrites. Chondrites contain millimetre-sized beads made essentially of silicates that are called chondrules (Greek *chondros* = grain) (Figure 1). The origin of chondrules remains enigmatic, but they are accepted as some of the early solids in the Solar System. Chondrites are gas-borne agglomerates, of both high- and low-temperature materials whose individual components and whole rocks have been variably altered by retrograde (aqueous alteration) and prograde (recrystallisation) metamorphism. In many chondrites, secondary (metamorphic) processes have been overprinted by tertiary (shock metamorphic) events.

Essentially, there are only two major categories of meteorites: meteorites that contain chondrules, the chondrites, and the non-chondritic meteorites that do not. The non-chondritic meteorites include those meteorites that lack chondrules and have textures and chemistries that show that they formed by partial, or complete igneous differentiation on their parent bodies, or are breccias of igneous debris. They include two kinds of stony achondritic (silicate-rich, but lacking chondrules) meteorites; primitive achondrites (those that retain a chemical signature of the precursor chondritic material from which they were made), and excluding meteorites from the Moon and Mars, highly differentiated asteroidal achondrites. Of the metal-rich meteorites, there are iron meteorites with essentially igneous histories; and two distinct groups of igneous stony-irons, mesosiderites and pallasites. In addition, there are a number (~60) of meteorites (mainly irons) that do not fit into any of the recognised groups and are termed ungrouped.



Figure 1 Barred olivine chondrule in the Allende CV3 carbonaceous chondrite (field of view 2 mm).

In the modern classification of meteorites 15 groups of chondrites, three groups of primitive and seven groups of highly differentiated asteroidal achondrites, four groups of martian achondrites, lunar achondrites, four groups of stony-irons (mesosiderites and three subgroups of pallasites), and 13 groups of irons are recognised, and together with ungrouped meteorites represent material from at least 130 parent bodies that had independent histories since the birth of the Solar System (Tables 1, 2).

METEORITES IN AUSTRALIA

The first well-documented recoveries of meteorites in Australia were two large masses of iron weighing 3.5 and 1.5 t found in 1854 near Cranbourne in Victoria. An earlier discovery may have been the Barratta stony meteorite, reported to have been found in 1845 in Townsend County, New South Wales (Liversidge 1872), but Mason (1974) suggested the date of find cannot be confirmed. A description of the Cranbourne meteorites by Von Haidinger (1861) marked the beginning of research on Australian meteorites, although in this case not in Australia. Subsequently, during the period 1854–1928, eight additional masses of the Cranbourne meteorite shower were recovered from an area between Beaconsfield and Langwarrin bringing the total weight

recovered to more than 10 t. Extensive literature on the Cranbourne irons has been summarised by Edwards & Baker (1944) and, more recently, by Grady (2000).

The most prominent scientist involved with the early description of meteorites from Western Australia was Edward Sydney Simpson (1875–1939). Simpson was appointed as Mineralogist and Assayer to the Geological Survey of Western Australia in 1897. A graduate of the University of Sydney, later Simpson enrolled at the University of Western Australia (UWA founded in 1911) (Glover 2003). With a credit from his degree in Mining and Metallurgy from the University of Sydney, Simpson was conferred with his degree in Geology in 1914 after only two years and became the first graduate of UWA.

Meteorites found in Australia have been reviewed, or listed, on numerous occasions in the past (Cooksey 1897; Anderson 1913; Prior 1923; Hodge-Smith 1939; Prior & Hey 1953; Hey 1966; Mason 1974; Gibbons 1977; Graham et al. 1985; Bevan 1992a; Grady 2000). Currently, data on 735 distinct meteorite recoveries from Australia are recorded in world-listings and many of these discoveries (91) were recovered from the Nullarbor Region, in Western Australia and South Australia. For climatic and geological reasons the Nullarbor Region has proved to be one of the most prolific areas of the world for meteorite recoveries outside of Antarctica (Bevan & Binns 1989a, b, c; Bevan 2006). Since 1985, systematic searching in the Western Australian Nullarbor has yielded several hundred stony meteorites many of which have yet to be described. Currently, described meteorite recoveries from Western Australia account for nearly half (350) of all meteorites known from Australia, including the largest known (Figure 2).

THE SCIENCE AND THE SCIENTISTS

Undoubtedly the largest and most active meteorite research group in Australia in the 1950s and 1960s was at the Australian National University. The group at various times included John Francis Lovering, Stuart Ross Taylor, William Compston and Alfred Edward (Ted) Ringwood (1930–1993), all of whom made major contributions to the study of planetary materials.

Moon

At various times, Lovering, Taylor, Ringwood and Compston separately worked on meteorites and, from 1969, were heavily involved in the study of samples returned from the Moon. In July 1969, Taylor, then at NASA in Houston, Texas, was the first scientist to analyse a sample of the Moon returned by Apollo 11. A New Zealand born petrologist and geochemist, Taylor's supervisor at NASA was Robin Brett, a South Australian. A byproduct of that first analysis of a lunar basalt was that it proved beyond doubt that tektites (distal terrestrial impact melt ejecta) could not have come from the Moon as had previously been proposed (see Taylor 1973 and references therein).

In the 1970s, Lovering, then Professor of Geology at the University of Melbourne, employed David A Wark (1939–2005) as his research assistant. Working on lunar basalt samples from the Apollo 11 mission, and using Lexan fission track maps, Wark (with Lovering) co-



Figure 2 The Mundrabilla iron meteorite (group IAB-complex) was found on the Nullarbor Plain in 1966. At 12.4 t it is the largest known from Australia.

discovered a hitherto unknown mineral, tranquillityite [Fe²⁺₈(ZrY)₂Ti₃Si₃O₂₄] (Lovering *et al.* 1971). Later the same mineral was found in rocks from other Apollo missions and, more recently, in terrestrial rocks from Western Australia (Rasmussen *et al.* 2011). Using Lexan and additional techniques, other mineral phases in lunar rocks were characterised, such as zirconolite (Wark *et al.* 1973) and monazite (Lovering *et al.* 1974).

Compston, a geophysicist and a graduate of the University of Western Australia, moved to the Research School of Earth Sciences (ANU) following his PhD on carbon isotopes under the supervision of Peter Jeffery (1922–1990). After Compston, Jeffery supervised other students including John De Laeter (1933–2010) and Malcolm McCulloch both of whom later became prominent in the field of planetary science.

At ANU Compston continued his isotopic work on dating rocks. During the Apollo era he was a principal investigator of a group studying the ages of lunar rocks. Using the ⁸⁷Rb–⁸⁷Sr dating technique that he had previously applied to terrestrial rocks, Compston's group obtained an age of 3.8 Ga from the mesostasis (the last fraction of magma to crystallise) of a lunar basalt (Compston *et al.* 1970).

Chemistry, mineralogy and petrology of the chondrites

The earliest attempts to classify the chondrites relied solely on texture. However, in 1916 G T Prior [British Museum (Natural History)] proposed a mineralogical classification and assigned the chondrites to three categories, enstatite, olivine–bronzite, and olivine–hypersthene on the basis of the Fe content of low-Ca pyroxene (Prior 1916, 1920). During the 1950s and 1960s, with improvements in the accuracy of analytical methods, a robust classification of the chondrites started to emerge. Chondrite groups not only differ in oxidation state, but significant differences also exist between the abundances of major, non-volatile elements they contain. This was demonstrated for Fe in chondrites by Urey & Craig (1953), who recognised two groups at around 22 wt% and 28 wt% Fe. These groups encompassed Prior's

enstatite chondrites and olivine-bronzite chondrites, and an additional category (Mason 1962), carbonaceous chondrites (all high-Fe), and the olivine-hypersthene chondrites (low-Fe). Further detailed analysis showed that enstatite, ordinary and carbonaceous chondrites differ in the ratio of Mg/Si (Ahrens 1964, 1965). Further, Von Michaelis et al. (1969) showed that they also differ in Ca/Si, Ti/Si and Al/Si ratios. From the 1960s the accumulation of quality mineralogical analytical data, mainly using non-destructive methods such as the electron microprobe, led to the recognition of a small number of chondrites that were largely unaltered and contained unequilibrated minerals (Dodd & Van Schmus 1965; Schmitt et al. 1966; Binns 1967a). This led to classification of the chondrites by degree of crystallisation, culminating in a chemical-petrologic classification (Van Schmus & Wood 1967). The classification divides chondrites into groups E (enstatite chondrites), H (high-iron chondrites), L (low-iron chondrites), and LL (low total iron, low metallic iron chondrites) (Table 1). The H- L- and LL-chondrites are collectively known as 'ordinary chondrites'. Within each chemical group of chondrites, meteorites show varying degrees of crystallisation from least (type 3) to most (type 6) crystallised, with types 4 and 5 intermediate to these extremes. Types 1 and 2 refer to carbonaceous chondrites that have suffered hydrothermal alteration (Van Schmus & Wood 1967).

During the 1960s, R A (Ray) Binns then at the University of New England, and later at the University of Western Australia (1971–1977), conducted research into many aspects of the mineralogy and petrology of chondritic meteorites. Along with Van Schmus & Wood (1967), Binns recognised the importance of distinguishing between chondrites with similar chemical compositions but with different textures (Binns 1967a, b). The relationship between type 3 (unequilibrated chondrites) and types 4–6 chondrites was then a much disputed subject. Through detailed studies of the composition and crystallography of pyroxenes from non-carbonaceous chondrites, Binns (1967a, 1970), along with others, recognised the mineralogical distinction between

Table 1 Meteorite classification: chondrites.

Class	Group	Petrologic type	Subgroup	Mg/Si at*	Fe/Si at*
Carbonaceous (C)	CI	1	_	1.066	8719
	CM	1-2	_	1.042	8177
	CO	3-4	_	1.053	7847
	CV	3-4	CVa, CVb, CVred	1.066	7578
	CK	3-6	_	1.127	7855
	CR	1-3	_	1.045	7875
	CH	3	-	1.063	15222
	СВ	3	CBa, CBb	-	-
Ordinary (OC)	Н	3-6	_	0.954	8177
	L	3-6	_	0.952	5838
	LL	3-6	-	0.928	4913
Enstatite (E)	EH	3-6	_	0.871	8730
	EL	3-6	-	0.731	5934
	R (Rumuruti)	3-6	_	0.934	7696
	K (Kakangari)	3	_	_	_

^{*} Data from Hutchison 2004

unequilibrated and equilibrated chondrites correlated with textural variations, and that the range of properties found within each chemical–mineralogical group of chondrite could be interpreted as reflecting varying degrees of post-accumulation recrystallisation. The unequilibrated chondrites largely avoided recrystallisation, and represent the kind of material from which equilibrated chondrites were derived by prograde metamorphism on their parent bodies (Van Schmus & Wood 1967; Binns 1967a; Dodd 1969). These studies led to a greatly improved petrographic and genetic understanding of the chondrites.

The origin of the chondrules that make up the greater portion of the chondrites remains a matter of debate to the present day. However, early workers recognised that chondrules crystallised from molten droplets very early in the history of the Solar System (Hutchison 2004 and references therein). The heat sources to produce the chondrules, and to progressively metamorphose the chondrites also remain a matter of debate. However, there is wide consensus today that the heat source for metamorphism was the decay of short-lived radionuclides such as Al²⁶ (McKeegan & Davis 2005 and references therein).

In the late 1950s, early 1960s, Ringwood, then at ANU in Canberra, began documenting the mineralogy and chemistry of groups of chondrites. He postulated that several meteorite groups had formed by 'auto-reduction' of CI chondrite (formerly known as Type 1 carbonaceous chondrite), and concluded that the various suites of differentiated meteorites had formed by melting and differentiation of chondrite precursors (Ringwood 1961). Ringwood also formulated what became known as the 'Chondritic Earth Model' and discussed the composition and origin of the Solar System publishing extensively on the subject. Ringwood emphasised the importance of different oxidation states of primordial condensed matter of chondritic composition to account for different

densities between Venus, Earth and Mars (Ringwood 1959, 1960, 1962). His study of meteorites also took Ringwood to Sweden where he worked with Kurt Fredriksson on chondritic meteorites, culminating in a paper on the origin of chondrules (Fredriksson & Ringwood 1963) and later, the origin of chondrites (Ringwood 1966).

In 1969, a new mineral was discovered in shockinduced melt veins in the Tenham ordinary chondrite from Queensland (Binns et al. 1969). The mineral, named ringwoodite in honour of the work of Ted Ringwood, is a high-pressure polymorph of olivine with a spinel structure. Ringwoodite is thought to be the most abundant mineral phase in the lower part of the Earth's transition zone (525-600 km), and its structure and chemistry partly determine the properties of the Earth's mantle at those depths, and had previously been synthesised by Ted Ringwood and Alan Major at ANU in 1966 (Ringwood & Major 1966). Later, in 1970, another high-pressure polymorph, this time of pyroxene with a garnet structure, was discovered in shock veins in the Coorara ordinary chondrite from the Western Australian Nullarbor (Smith & Mason 1970). The mineral was named majorite in honour of Alan Major and was later synthesised in the laboratory (Ringwood & Major 1971). A second high-pressure polymorph of olivine with an orthorhombic structure was found in the Peace River ordinary chondrite from Canada (Price et al. 1983). The mineral, wadsleyite, was named in honour of Arthur David Wadsley (1918-1969), and had previously been synthesised as a stable compound by Ringwood & Major (1966). Magnesian olivine α-Mg,SiO, under certain temperature and pressure conditions transforms to wadsleyite β-Mg,SiO, and with increasing pressure transforms to ringwoodite γ-Mg₂SiO₄. In addition to an understanding of shock metamorphism in ordinary chondrites, an experimental understanding of these transformations has greatly improved our knowledge of the nature and properties of the Earth's mantle.

Table 2 Meteorite classification: non-chondritic meteorites

Pi	rimitive achondrites		
Acapulcoites Lodranites	Clan/same parent body?		
Silicates in IAB-complex irons Winonaites	Clan/same parent body?		
	erentiated achondrites hondrites (asteroidal)		
Angrites	monumes (asteroidar)		
Aubrites			
Brachinites			
Ureilites			
Howardites			
Eucrites	HED clan, same parent body		
Diogenites			
Ac	chondrites (planetary)		
Shergottites			
Nakhlites	Martian (SNC)		
Chassignites	(SINC)		
Orthopyroxenites	J		
Lunar	Moon		
	Stony irons		
Mesosiderites	Possible related to HED clan		
•	Main group Possible related to IIIAB irons		
Pallasites	Eagle Station		
	Pyroxene		
	Irons		
IAB-complex*			
IC			
IIAB			
IIC			
IID			
IIE*	Possible differentiates from H-chondrite-like precursor		
IIF			
IIG			
IIIAB	Possibly related to Main group pallasites		
IIIE			
IIIF			
IVA*			
IVB			
Ungrouped			

^{*} Silicate-bearing irons

Mineralogy, petrology and the characterisation of calcium-aluminium-rich inclusions in chondrites

While texturally most chondrites are dominated by chondrules and the matrix in which they are set, mineralogically they are complex aggregates of ferromagnesian silicates (olivine and pyroxene), Fe–Ni metal, Ca–Al-rich inclusions (often referred to as refractory inclusions, or CAIs), and rare aggregates of olivine grains (amoeboid olivine aggregates). Additionally, the mineralogy of chondrites may include magnetite, chromite (or chrome spinels), iron sulfides (troilite, pyrrhotite and pentlandite), carbonates, sulfates and

'serpentine' group minerals (for a detailed review of meteorite mineralogy see Rubin 1997a, b).

Ca-Al-rich inclusions contain refractory materials and range in size from sub-millimetre, to centimetre-sized, objects that occur in varying abundances in all groups of chondrites (Figure 3). The mineralogy and isotopic composition of Ca-Al-rich inclusions suggest that they are amongst the earliest solids to have formed in the Solar System, and this is confirmed by isotopic dating. Both Ca-Al-rich inclusions and chondrules are the products of very high temperature events during the early history of the Solar System, and the latter probably



Figure 3 Large white calcium-aluminium-rich inclusion (CAI) in the CV3 chondrite Allende (bottom right); centimetre scale,

originated from pre-existing solids in the nebula (MacPherson 2005; Rubin 2000; Shu *et al.* 2001).

Brian Harold Mason (1917–2009), a New Zealand born geochemist/mineralogist visited Ross Taylor's laboratory at ANU in the 1970s and made one of the most siginificant contributions to the study of CAIs. Analysing inclusions in Allende and based on their REE contents and mineral make up, Mason established a classification of CAIs into groups. Four distinct groups were recognised and designated I, II, III and IV, that indicated a complex history of formation from the ancestral nebula (Martin & Mason 1974; Mason & Martin 1977; Mason & Taylor 1982). This work was later superseded by MacPherson *et al.* (1988) who distinguished a number of 'types' of CAIs on the basis of their texture, primary mineralogy and composition.

In the 1970s and 80s, both Lovering and Wark also made major contributions to the understanding of the mineralogy of CAIs. In the Allende CV3 carbonaceous chondrite, thin layers each $5\text{--}10\mu m$ thick (rims) and total thickness 20-50µm of spinel plus perovskite, alteration products, and pyroxene are ubiquitous on coarse CAIs. This sequence of layers is identical to that making up the individual bodies in fine-grained aggregates (Wark & Lovering 1977). In honour of their work, these layers later became universally known as 'Wark-Lovering' rims (MacPherson et al. 1998). This detailed work on CAI rims fostered many other lines of inquiry into their origin, which remains uncertain to the present day. Wark & Lovering (1977) demonstrated that the second alteration layer, composed of nepheline, grossular and sodalite, had originally been melilite. In less-altered meteorites, rims show the primary melilite layer (Wark & Lovering 1980).

In later work, Wark (1985) classified CAIs according to both chemistry and petrology, and provided a review of rim formation (Wark & Boynton 2001). Wark's work on CAIs culminated in experimental methods to synthesise them in the laboratory, summarised by Wark (2005).

An Australian role in the classification and understanding of iron meteorites

Until the 1950s iron meteorites were classified according to their structural characteristics and were assigned to eight classes. Octahedrites (5.6–18.1 wt% Ni), are those irons (6 classes) with discernable Widmanstätten patterns composed principally of a trellis work of the Fe–Ni minerals kamacite and taenite (Figure 4), hexahedrites (5.3–5.8 wt% Ni) lack the octahedrite structure and are essentially made of crystals of kamacite, while ataxites (15.8–60.8 wt% Ni) have microscopic octahedral structures. It was generally recognised that among iron meteorites there was an inverse relationship between the bulk content of Ni in irons and the bandwith of kamacite lamellae in the Widmanstätten pattern.

Michael J Frost, who gained a PhD from the University of Western Australia and later moved to the University of Cantebury in New Zealand, developed a rapid, easy method for the determination of kamacite bandwidths in iron meteorites, thereby determining their structural class (Frost 1965). On an etched section of an iron meteorite which is not normal to any one of the four sets of octahedral kamacite lamellae, the apparent width of kamacite bands will be greater than the true thickness. Depending on the orientation of the section plane there will be 4, 3, or 2 sets of kamacite lamellae. Using tracing paper, through a single point lines are drawn parallel to the sets of lamellae. In the case of 4 sets, the width of the narrowest bands are measured to give an average value. The largest angle between adjacent lines on the tracing paper is measured, and the average apparent bandwidth is multiplied by a correction factor (cf) appropriate to the maximum angle (60-62° cf 0.97; 64-66° cf 0.98; 68° cf 0.99; 70° cf 1.00; 90° cf 0.82). In the case of 3 sets, two angles will be the same or similar and the third angle will be unique. The apparent bandwidths of the two sets of lamellae that include the unique angle are measured. The weighted mean of the two averages is then multiplied by an appropriate correction factor (unique angle 10° cf 0.82; 20° cf 0.83; 30° cf 0.85; 40° cf 0.87; 45° cf 0.88; 50° cf 0.90; 55° cf 0.92; 60° cf 0.94; 63° cf 0.96; 66° cf 0.97; 68° cf 0.98; 70° cf 1.00). Finally, in the case of two sets, the apparent average width of the two sets is measured and the weighted mean of the two averages is multiplied by cf 0.82 (Frost 1965).

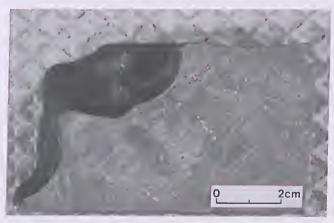


Figure 4 Polished and etched slice showing the Widmanstätten pattern in the medium octahedrite (chemical group IIIAB iron) Duketon, found in Western Australia.

Through the 1950s, as analytical equipment improved, the amount and accuracy of major, minor, and traceelement data for iron meteorites increased and a chemical classification emerged by grouping apparently chemically related irons. The earliest work was done at the California Institute of Technology (Caltech) by Goldberg et al. (1951) who discovered that the Ga contents of 40 irons lie within three discrete ranges. On the basis of this they assigned Roman numerals to classes I, II and III. In 1953, Lovering joined the group at Caltech and continued the work (Lovering et al. 1957). Lovering et al. (1957) showed that the group with the highest range of Ga contents could be subdivided into two, and that Ga contents correlated with Ge. From trace-element data derived from the analysis of 88 irons, four groups were recognised in order of decreasing Ga and Ge and designated groups I to IV. Eleven irons fell outside the limits of any group and were considered anomalous. This notation forms the framework for the chemical classification of iron meteorites in use today.

From the mid-1960s, analysis of iron meteorites was taken up by J T Wasson and colleagues at the University of California in Los Angeles. Using more sensitive and precise analytical techniques, Wasson and co-workers have analysed >700 irons. Chemical comparisons between chondritic and iron meteorite metal show that, overall, irons have much wider compositional ranges for most elements. Notable are the trace-elements Ga, Ge and Ir. However, plots of Ga, Ge and Ir versus Ni distinguish 13 well-defined groups of irons and form-the basis of a chemical classification (Goldberg et al. 1951; Lovering et al. 1957; Scott & Wasson 1975, 1976; Scott 1979; Kracher et al. 1980; Goldstein et al. 2009). Some 13% of irons (around 60) have compositions that do not fit into the groups. These were previously called anomalous, but are now called ungrouped. This work has provided a genetic classification that has led to major advances in the understanding of the interrelationships among iron meteorites (and other groups of meteorites) and their origin and evolution (see Goldstein et al. 2009 and references therein).

Chemical variations between groups of irons were probably established in chemically distinct environments (parent bodies) by processes similar to those which determined metal chemistries in chondritic meteorites (Scott 1979), whereas the regular chemical variation within groups of irons are attributed to the gravitational separation and subsequent crystallisation of molten metal during planetary differentiation (Scott 1972 & 1979; Kelly & Larimer 1977; Goldstein et al. 2009). Chemical trends (for Ni, Ga, Ge, Ir) in most iron meteorite groups are broadly consistent with fractional crystallisation of a single molten metallic core, and are called 'magmatic irons'. In contrast, irons of the group IAB complex (including those formerly labelled IIICD) lack extreme magmatic chemical fractionation trends and contain silicates, some with chondritic chemistries (Bunch et al. 1970; Benedix et al. 2000) indicating that they were never completely melted (Kracher et al. 1980). The group IAB complex of irons are undoubtedly the products of some melting, although compositional changes resulting from partial melting and incomplete separation of metal and silicate are poorly understood. Kelly & Larimer (1977) suggested that some groups of irons such as IAB may

represent the products of fractional melting (the inverse of fractional crystallisation), but there is no consensus. The modern view is that non-magmatic irons such as the IAB-complex and group IIE that are silicate-bearing and with poorly defined chemical trends, are perhaps the result of impact-mixing of molten metal and silicates, and that neither group formed from a single, isolated metallic melt (Goldstein *et al.* 2009).

Lovering (1957) suggested that mechanisms for the macrosegregation of elements in the cores of meteorite parent bodies imply that solidification may have been directional. Directional solidification is supported by elongated, parallel troilite nodules that occur in some irons. Both 'plane front' (Scott 1972) and 'dendritic' (Narayan & Goldstein 1982) solidification have been considered to account for elemental fractionations shown by the magmatic iron meteorite groups. However, computer modelling indicates that plane-front solidification is unstable in large molten metallic accumulations with moderate thermal gradients and solidification rates, and predicts dendritic solidification for irons.

'As cast' solidification structures are rarely seen on sections through average sized iron meteorites (<1 m) because the dendrite arm spacing on the scale of planetesimal cores may have been up to 0.5 km. The solubility of S in solid Fe-Ni is very low (<0.8 wt%) consequently, during solidification, S remains in the melt. In the pure Fe-Ni-S system troilite (FeS) begins to crystallise when the S content of the melt reaches 45 atom% and is concentrated where the last liquid solidifies. Solidifying Fe-Ni dendrites may randomly trap sulfur-rich interdendritic material, and this has been suggested as a mechanism to account for observed variations in the sulfide contents of magmatic irons. Meteorites that may represent interdendritic material include the sulfide-rich ungrouped iron Soroti, and the IAB complex irons Pitts, Mundrabilla, and the recently discovered iron from Western Australia, Prospector Pool (Figure 5).



Figure 5 Mixture of metal and troilite (dark) in a slice of the Prospector Pool iron meteorite (group IAB-complex) found in Western Australia (largest dimension 8 cm).

Cohenite formation in iron meteorites

The iron-nickel carbide, cohenite (FeNi)₃C, is a common accessory precipitate in some groups of iron meteorites, notably the IAB complex and group IC. For example, in group IAB irons cohenite precipitates frequently occur associated with kamacite lamellae in the Widmanstätten pattern (Scott 1977). In some irons, cohenite has decomposed to granular ferrite and columnar graphite indicating mild reheating, or annealing during cooling. The morphological development and thermal history of cohenite is generally poorly understood. Cohenite is thermodynamically unstable. Buchwald (1975) noted that it is surprising that, given the slow, equilibrium cooling histories of many iron meteorites, cohenite survives at all. In iron meteorites generally, undecomposed carbides are more common than decomposed ones. Buchwald (1975) suggested that the apparent stability of cohenite is actually due to the difficulty of nucleating graphite. Robin Brett, then working at the US Geological Survey in Washington, noted that once nucleated in cohenite, however, graphite grows slowly at the expense of carbides with low-Ni ferrite as a byproduct and this seems dependent on the fractured nature of grains (Brett 1967). Annealing of shocked, strained and fractured cohenite causes it to decompose to ferrite and graphite. The temperature of heat treatment for this transformation is ~450-500°C.

From Fe-C phase equilibria and kinetic data, Brett (1967) showed that cohenite that formed in irons with <6 wt% Ni should decompose on cooling. Cohenite probably forms over a temperature range of 650-610°C during cooling, and P has a stabilising influence on its precipitation (Brett 1967). In meteorites containing up to 6 wt% Ni, regardless of the C content, all the cohenite would have precipitated from solid solution when the temperature had fallen to approximately 640°C (Brett 1967). The inability to form cohenite below approximately 610°C accounts for the lack of this phase in irons containing more than about 8 wt% Ni. Cohenite that formed at temperatures above 640°C should decompose on slow cooling. If cohenite does not form below 610°C then the only unaltered cohenite that persists in irons is in those containing 6-8 wt% Ni (Brett 1967).

In experimental heating of samples of the group IAB complex iron Canyon Diablo, Brentnall & Axon (1962) observed no apparent effect on cohenite in samples heated at 501°C for 24 hrs. Between 501 and 650°C, with heating periods varying from 15 mins to 6 hrs, a thin rim of ferrite developed around cohenite, and in a sample heated to 650°C for 3 hrs, incipient graphitisation occurred in cracks and veins. However, Brentnall & Axon (1962) noted that cohenite is generally unstable over the whole temperature range (300–1000°C) examined.

In order to establish the conditions of cohenite stability and the kinetics of its decomposition, Brett (1967) also performed heating experiments at three temperatures, 650, 750 and 800°C on samples of the cohenite-bearing IAB-complex iron Coolac that was found in New South Wales. In any given run, decomposition was more advanced in fractured cohenite grains, and decomposition first occurred along fractures, and then within crystals. Decomposition was complete in a sample

of Coolac held at 650°C for 80 days. Brett (1967) noted the duration of runs in which total decomposition of cohenite had occurred and plotted the data along with those obtained previously by Ringwood & Seabrook (1962) thus contributing to our knowledge of the low temperature cooling history of irons.

Opaque mineralogy of meteorites

The eminent German mineralogist Paul Ramdohr (1890–1985) visited the University of New South Wales in May 1962, and spent five months working with L J (Lawrie) Lawrence as a Visiting Professor of Geology. During this period, Ramdohr examined the opaque mineralogy in a suite of 17 meteorites provided by Oliver Chalmers, Curator at the Australian Museum in Sydney (Sutton 2012).

The meteorites included Adelie Land, the first meteorite found in Antarctica, and 12 chondrites, one achondrite, two pallasites, and a troilite nodule from an iron meteorite, all from localities in New South Wales (Ramdohr 1967).

As the result of Ramdohr's observations on meteorites, eight minerals which were known from terrestrial occurrences, though not previously from meteorites, were found to be fairly common constituents; others were recognised as accessory although had previously been considered rare. The latter included native copper and ilmenite. About 15 components were established that were previously not known as either terrestrial or meteoritic (Sutton 2012).

Isotopic studies

Through the 1960s interest in meteoritics grew in Australia. In Western Australia a group of physicists at the University of Western Australia led by Peter Jeffery, obtained a mass spectrometer and began to search for isotopic anomalies of tin in meteorites (De Laeter & Jeffery 1965). In addition, this research group encouraged Gerald Joseph Home (Joe) McCall (1920-2013), a geologist at the University of Western Australia, to classify the stony meteorites in the collection of the Western Australian Museum, whilst De Laeter undertook a similar task for iron meteorites in the collection (De Laeter & Bevan 1992 and references therein). An X-ray fluorescence spectrometry facility was established at Curtin University (then the Western Australian Institute of Technology) to measure the nickel, cobalt, gallium and germanium contents of iron meteorites, and so determine their chemical classification (Thomas & De Laeter 1972).

The vintage year for planetary science was 1969. On 20 July NASAs Apollo 11 mission succeeded in placing a man on the Moon, but at either end of the same year and on opposite sides of the Earth two meteorite falls had a more profound effect on our understanding of the origin of the Solar System. On 8 February more than 2 t of fragments of a CV3 (Vigarano-type) carbonaceous chondrite fell near the Mexican town of Peublito de Allende. On 28 September ~0.5 t of fragments of a CM2 (Mighei-type) carbonaceous chondrite fell near the Australian town of Murchison in Victoria. Of groups previously known in only meagre amounts, the Murchison and Allende meteorites provided an abundance of material to work on.

More than a decade before the falls of Murchison and Allende, Burbidge *et al.* (1957) drew up a blueprint of nuclear reactions in stars that would produce all but a few of the elements and isotopes. Cameron (1957) came to similar conclusions independently. Shortly after the birth of the Universe, stars manufactured isotopes of the chemical elements. Massive stars with burnt-out iron cores become unstable, eventually exploding as supernovae and distributing newly formed isotopes into space. New generations of stars form and the process continues. In this view of the Universe, isotopic mixes of elements should vary in space and time. By the 1960s the search for corroborating isotopic anomalies in meteorites had begun in earnest.

The first indication that the proto-solar nebula had been seeded by debris from a nearby supernova came in 1960. Reynolds (1960) extracted a small amount of xenon gas from the Richardton ordinary chondrite that fell in the USA in 1918, that was found to contain more of the isotope ¹²⁹Xe than predicted. The excess was attributed to the decay of the extinct radioactive isotope ¹²⁹I with a half-life of only 16 Ma. ¹²⁹I was made in a supernova shortly before it was incorporated into the meteoritic material. Because the daughter ¹²⁹Xe had not been lost to space, the material must have cooled quickly. For the record to have survived, no more than around 170 Ma (around 10 half-lives) could have elapsed between the manufacture of ¹²⁹I and the birth of the Solar System at 4.56 Ga. This was confirmation that young material had been added to the early Solar System.

Of the many isotopic anomalies discovered subsequently, one of the most significant is 26Mg as the decay product of the short-lived radioactive isotope 26Al with a half-life of 0.73 Ma. As early as 1952, Urey (1952) suggested that the decay of 26Al in the early Solar System could have been the source of heat for melting and differentiation of planetesimals. A concerted search for evidence of an excess of 26Mg in meteoritic materials started in the early 1970s. Schramm et al. (1970) found no anomalies in several meteorite samples. However, in 1974 two Australian scientists, Chris M Gray (Latrobe University) and William Compston (ANU) reported an excess of 26Mg in the Allende meteorite (Gray & Compston 1974), but their published results were regarded as inconclusive by American scientists working in the same field. This led Compston's colleague, Ringwood at the ANU to remark that this was 'uncharitable and reflects the chauvinism of U.S. scientists' (Brush 2006). Ringwood argued strongly that Gray and Compston's discovery of a 26Mg anomaly should receive the credit it deserved. Later, Lee et al. (1976) at Caltech discovered a large anomaly in 26Mg in a chondrule from the Allende meteorite, and suggested that the most plausible cause of the anomaly was the in situ decay of 26Al.

Geochronology

Since the late 1970s, the development of ever more sensitive and accurate means of determining absolute ages of materials has led to a new generation of instruments. The most significant was the development of the Sensitive High-Resolution lon Microprobe (SHRIMP). The SHRIMP originated in 1973 through a proposal by William Compston to build an ion

microprobe at the Research School of Earth Sciences at the ANU in order to analyse individual mineral grains. The instrument was built during the period 1975–1977 and the first successful geological measurements were made in 1980 (Foster 2010 and references therein).

Shortly after, in 1983, the first major scientific discovery using the SHRIMP was the dating of zircon grains in rocks from Mt Narryer in Western Australia at >4000 Ma (Froude et al. 1983), then at nearby Jack Hills (Compston & Pidgeon 1986). Interest from commercial companies and other research groups, notably John De Laeter's group at Curtin University, led to a project to build commercial versions of the instrument. Today 15 instruments have been installed in laboratories around the world, including those at ANU and Geoscience Australia in Canberra, and two at Curtin University in Perth. The development of the SHRIMP has allowed advances in the accuracy of the chronology of meteorites and their components, and the instrument's high sensitivity and resolution can be used to measure REE and other trace elements in individual grains. The first SHRIMP at Curtin University was commissioned in 1993 and Allen K Kennedy returned to Australia from the US to run the instrument.

The development of the first SHRIMP, and the discovery of the oldest zircons, brought forth a new generation of scientists including Trevor R Ireland, Peter D Kinny (now at Curtin University) and D O Froude who were then students at ANU.

Meteorite collecting and collections in Australia

In Australia, meteorite collections are held in all the State museums (including the Northern Territory). In addition, significant collections are held at some of Australia's universities, notably the Australian National University and the University of Melbourne. Other collections are held at Geoscience Australia in Canberra and CSIRO. One of the largest collections is held at the Western Australian Museum, a major component of which are meteorites recovered from the Nullarbor Region, and include several hundred meteorites that are yet to be classified and described (Bevan 2006).

In the 1960s, a major contribution to the collection of meteorites was made by an active group of scientists at the Western Australian School of Mines (now part of Curtin University) in Kalgoorlie. The principal researchers were William (Bill) Harold Cleverly (1917–1997) and M Keith Quartermaine, both of whom undertook meteorite collecting. During the decade of the 1960s almost a tonne of meteoritic material was amassed by the School of Mines, or via the school into other collections (Cleverly 1993). The material included 37 new meteorites representing an increase of ~2% to meteorites held in collections world-wide at that time. The 1960s also saw the recognition of the Nullarbor Region as an area of meteorite accumulation with time (see Bevan 2006 and references therein).

In 1963, an expedition funded by the National Geographic Society left Sydney to search for meteorites and tektites throughout Australia. The search party consisted of Brian Mason (then at the American Museum of Natural History), Edward Henderson (Smithsonian Institution), and Oliver Chalmers (Australian Museum,

Sydney). In Western Australia they targeted the find-sites of two previously known meteorite finds; Dalgety Downs and Mount Egerton that had been discovered in 1941. The party relocated the find-site of Dalgety Downs and ~214 kg of material was recovered. A further visit to the site by Cleverly yielded another 40.9 kg of fragments (McCall 1966). The search for the find-site of the Mount Egerton meteorite by the National Geographic expedition was unsuccessful.

In 1986, a new meteorite recovery programme of the Western Australian Museum (WAMET) was initiated by the author. From 1992 to 1994, in collaboration with EUROMET, a pan-European group of research institutions devoted to meteorite research, systematic searches on four expeditions to the Nullarbor Region recovered more than 600 specimens of meteorites (totalling ~17 kg) during some 10 weeks of searching (Bevan 1992b; Bevan *et al.* 1998).

Meteorites and paleoclimate

In the 1990s, with the recovery of large numbers of stony meteorites of varying terrestrial ages and states of preservation from the desert regions of the world, it was realised that paleoclimatic information might be obtained from them by a study of their weathering characteristics (Bland *et al.* 2000). Philip A Bland (then a Royal Society Travelling Fellow at the Western Australian Museum), the author, and A J T Jull of the University of Arizona undertook an innovative study of the terrestrial oxidation (weathering) and terrestrial age of ordinary chondritic meteorites from several arid areas of the world, notably the Nullarbor Region in Australia.

At the moment of entry into the Earth's atmosphere, a meteorite is exposed to contamination from, and alteration by, the terrestrial environment. Prolonged weathering transforms many of the minerals in meteorites, masks their original textures, redistributes elements, and eventually leads to their destruction. The processes of weathering leave a terrestrial 'fingerprint' in meteorite finds that can be used in climatic research. Meteorites that have survived prolonged weathering are 'recorders' of environmental conditions during their period of terrestrial residence.

Ordinary chondritic meteorites are particularly useful in understanding post-fall terrestrial processes for two main reasons. First, their terrestrial ages (the time they have spent on Earth since falling) can be measured (up to >40 ka) from the decay of the cosmogenically produced radionuclide 14C (half-life of 5.73 ka). The technique separates 14C produced by cosmic-ray bombardment in space from ¹⁴C contamination from terrestrial sources (see Jull 2006 and references therein). Second, the initial composition and normative mineralogy of ordinary chondrites prior to weathering is well constrained from the analysis of fresh falls (see Jarosewich 1990 and references therein). Virtually, all of the iron in equilibrated (types 5-6) ordinary chondrites is present as Fe⁰ and Fe²⁺. If an ordinary chondrite contains significant Fe3+ then this is an indication of terrestrial weathering by the oxidation of Fe-bearing phases (rusting).

Bland *et al.* (2000) used an empirical approach to quantify the nature and degree of weathering suffered by an ordinary chondrite by the use of ⁵⁷Fe Mössbauer

Spectroscopy to measure %age ferric oxidation in ordinary chondrites. By correlation of oxidation state with terrestrial ages, the progression of weathering with time was determined.

Logically it would be expected that the degree of weathering of a meteorite would increase with greater terrestrial age. In the case of the meteorite accumulation in the Nullarbor Region, Bland *et al.* (2000) found that this was not the case (Figure 6). In the Nullarbor Region peaks in total oxidation for ordinary chondrites correspond with humid periods identified independently from speleothem growth in caves (Goede *et al.* 1990), palynology (Martin 1973) and lake-level studies (Street & Grove 1979; Bowler *et al.* 1976; Bowler 1978). A peak in %age oxidation for H-group chondrites is observed at ~1500–1000 a BP. Lake-level studies also indicate a period of more effective precipitation at ~2000–1000 a BP, and halite speleothem growth occurred at 2500±1200 a BP.

A possible mechanism that allows variation in oxidation that is not directly dependent on increasing terrestrial age is that the weathering of an ordinary chondrite (<1000 a after fall) appears initially to be rapid before oxidation is arrested and weathering reaches equilibrium (Bland et al. 2000). The reduction in weathering rate may correspond to a reduction in porosity of the stone caused by the oxidation and mobilisation of Fe–Ni metal and other primary minerals to oxyhydroxides of iron that fill the pore space thus preventing the percolation of fluids, and inhibiting further weathering (Bland et al. 2000).

Essentially, the humidity during the period a meteorite falls is the major factor determining the degree of initial weathering. A meteorite will undergo more initial weathering in a humid environment than in an arid one. The reduction of porosity early in a meteorites terrestrial history greatly reduces the weathering rate, and even a lightly weathered meteorite may be unaffected by subsequent humid periods (Bland *et al.*)

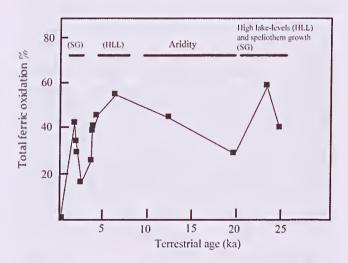


Figure 6 Plot of total ferric oxidation (%) resulting from the alteration of metallic iron by the terrestrial oxidation of weathered H-group ordinary chondrites from the Nullarbor Region of Australia as determined by Mössbauer against their ¹⁴C terrestrial ages. Marked above are significant paleoclimatic events in southwest Australia for the same period (after Bland *et al.* 2000).

2000). The use of ordinary chondrite meteorites recovered from desert regions in paleoclimatic research has yet to be fully explored.

AUSTRALIAN DESERT FIREBALL NETWORK

The newly established Australian Desert Fireball Network (ADFN) in the Western Australian Nullarbor is a world-leading facility designed to provide fundamentally important information to planetary scientists about the nature and origin of meteorites (Bland et al. 2012). Through an international collaboration led by Philip A Bland between Curtin University, Imperial College London, the Ondrejov Observatory in Prague, and the Western Australian Museum, construction of a trial all-sky camera network comprising four fireball observatories was completed in 2007 and enjoyed almost immediate success. A meteorite fall, Bunburra Rockhole, was photographed in July 2007 and was later recovered within 100 m of the landing site predicted by the network (Bland et al. 2009). A second recovered fall, Mason Gully, was photographed by the network on 13 April 2010 (Spurny et al. 2011).

Of the more than 50 000 meteorites in collections around the world, the vast majority are chance finds. Over the last 300 years or so, world-wide only about 1100 have actually been seen to fall and quickly recovered. Of these, the phenomena associated with the fall of only 16 have been photographed enabling the orbits of the objects that gave rise to the meteorites landing on Earth to be determined. Fragments of another meteorite fall were recovered by tracking a small asteroid that eventually collided with the Earth (Jenniskens *et al.* 2009).

Networks of all-sky cameras, designed to observe fireballs, calculate orbits and triangulate fall positions, have been established in several northern-hemisphere nations (USA and Canada) in the past, and one, the European Network, has been in operation for more than 40 years (Bowden 2006). Although hundreds of fireballs associated with large (>100 g) meteorites have been observed, remarkably only eight meteorites were recovered (the orbits of others were determined from chance photography). The poor success rate is explained simply by the location of the networks. Heavy vegetation, typical of central Europe, makes locating small meteorites difficult. Until now, no camera network has been established in an area, such as a desert, where meteorites can be recognised easily and quickly recovered. The climate of southwestern Australia is also conducive for observations with around 200 clear nights per year.

Four satellite-monitored cameras specifically designed to operate in extreme desert conditions have been deployed in the Nullarbor (Figure 7). Orbits are calculated from fireballs, and meteorite fall positions (over an area of ~200 000 km²) are determined for later recovery. Data from the current network indicate that three to four meteorite falls are detected per year. In the sparsely vegetated Nullarbor, it is expected to recover a significant proportion of those photographically recorded meteorite falls, which will greatly increase the number of recovered meteorites with known orbits.

At present there is only an approximate knowledge of where most meteorites come from. Surveys of light reflected from asteroids reveal a diversity of bodies, each with a distinct inferred surface mineral make-up. An expanded collection of meteorites with known orbits will allow the relationship of some samples to specific regions, or bodies, providing a spatial context for interpreting meteorite composition.

The velocity of a meteoroid (a small natural body before landing on Earth) in the atmosphere is that of the object relative to the Earth (geocentric velocity). In order to calculate the orbit of the object in space the velocity of the object relative to the Sun (heliocentric velocity) at the Earth's distance from the Sun needs to be known. Taking into account the Earth's own orbital speed (29 km/s) and



Figure 7 A fireball observatory of the Australian Desert Fireball Network on the Nullarbor in Western Australia, with solar power and satellite link (Courtesy of Geoff Deacon).

the rate of rotation of the Earth (~0.5 km/s) it is possible to work back to obtain the dimensions and shape of the orbit of the infalling body. In all cases measured previously, the orbits of bodies that have given rise to recovered meteorite falls are highly elliptical with their furthest point from the Sun in the asteroid belt between Mars and Jupiter. This is strong evidence, albeit circumstantial, that the majority of meteorites that fall to Earth are fragments broken from asteroids.

On 20 July 2007, two cameras of the ADFN detected the fall of a meteorite. At 19hrs 13mins 53.2 secs (±0.1 sec) Universal Time, a fireball was recorded low on the horizon east of the network area, and the atmospheric trajectory, luminosity of the fireball, orbit, and impact position were determined precisely. The record also indicated that the body broke in the atmosphere to give at least three surviving fragments.

The successful recovery of three fragments (174, 150 and 14.9 g) of the Bunburra Rockhole meteorite fall represented a number of scientific firsts. At the time it was only the fifth predicted meteorite fall in history, it was the first known meteorite from an Aten-type asteroid orbit, the first basaltic achondrite with a known orbit, and the first instrumentally observed meteorite fall in the southern hemisphere. Moreover, it was the first documented meteorite fall from a relatively small object that produced a short-lived fireball with a terminal height of 30 km.

The Bunburra Rockhole meteorite has proved very unusual, not least of which is its orbit. The Aten asteroids are a group of near-Earth asteroids, named after the first of the group to be discovered (2062 Aten). Half of their largest orbital dimension is less than the distance from the Earth to the Sun. However, because the orbits of asteroids can be highly elliptical, the orbit of an Aten asteroid need not be entirely contained within Earth's orbit. Nearly all known Aten asteroids have orbits with their greatest distance from the Sun beyond the Earth's orbit, as did Bunburra Rockhole.

Although many other basaltic achondrites similar to Bunburra Rockhole are known and have been linked, tentatively, to asteroid 4Vesta and related bodies called the V-type asteroids as their parent bodies, Bunburra Rockhole appears to have come from a different region of space. Although its chemical composition is not significantly different from other basaltic achondrites, the isotopic make-up of its oxygen distinguishes it.

When the ratios of heavier isotopes of oxygen (¹⁷O, ¹⁸O) to light ¹⁶O in different samples from Earth are plotted against each other they lie on a line with a slope of exactly one-half. All Earth samples lie on this line, as do samples from the Moon. This is strong evidence that the Earth and the Moon are not chance associates, but formed from the same oxygen source in the same region of the Solar System. Any samples formed from another source of oxygen would lie on different lines. This is the case for Bunburra Rockhole. Not only did it form in a different region of the Solar System to the Earth and the Moon, it also appears to have formed in a different parent body from other similar basaltic igneous meteorites.

To date, the ADFN has recorded >550 fireballs. Of these, multi-station observations from which precise

atmospheric trajectories and orbits have been calculated number 150. This is the first set of data for southern hemisphere fireballs, and it is possible that a new, active meteor shower has also been discovered. Of the events recorded on multiple stations, around 11 may have resulted in meteorites, not all of which are recoverable. Four of these are probable falls with masses within the range 10-100 g, five are certain falls with terminal masses greater than 100 g, and one had an initial mass of 20 t. Unfortunately, this latter fall, which may have had a cometary origin, fell into the Great Australian Bight. One certain fall, and two probable falls are, as yet, unrecovered and lie in easily searchable areas of the Nullarbor. Three additional recent events are almost certainly recoverable falls and calculations to locate them are in progress, In October 2010 a fragment of one of these falls, Mason Gully, weighing 24.54 g was recovered marking the second success of the ADFN (Spurny et al. 2011). An H5 ordinary chondrite, Mason Gully may also be compositionally anomalous.

With the successful operation of the network, a milestone in meteoritics has been achieved. Having demonstrated the undoubted viability of the project, the ADFN has already become a major contributor to Solar System research.

IMPACT CRATERING

Meteorite impact is a significant geological process and the surviving impact record provides the only tangible evidence against which theoretical predictions of the effects of potentially catastrophic impact can be compared. Accumulating definitive evidence of impact is the most important aspect of crater studies. By establishing the impact origin of structures and determining their sizes and ages, the data can be used to calculate cratering rates with time, and predict the liklihood of another event occurring in future.

The first meteorite impact crater to be discovered in Australia was Dalgaranga in Western Australia in 1921. The structure was later confirmed as of impact origin by the discovery of meteorite fragments associated with the structure in 1923 (Simpson 1938). This discovery was followed by the discovery of meteorites at the Henbury craters (1931) and the Boxhole crater (1937) in the Northern Territory that confirmed their impact origin (Alderman 1932; Madigan 1937). At the time the only other craters known with associated surviving fragments of the projectile were Meteor Crater (1897) and Odessa (1922) both in the USA.

In 1947 the Wolfe Creek Crater (originally named Wolf Creek) was discovered from the air and later surveyed on the ground (Reeves & Chalmers 1949; Guppy & Matheson 1950). Wolfe Creek is the largest impact crater (~880 min diameter) associated with meteorites in Australia, and its discovery greatly heightened interest in impact studies.

Other, much larger, older and deeply eroded circular structures measuring tens of kilometres were recognised as of possible impact origin. Here no meteoritic material survived but evidence of intense shock-metamorphism and melting in the target rocks provided conclusive evidence of their impact origin.



Figure 8 Satellite image of Gosses Bluff, Northern Territory. The Bluff (top centre) is an eroded remnant of the central uplift of a complex impact crater. The overall diameter of the crater (pale area surrounding the Bluff) is 24 km (Courtesy of the Australian Centre for Remote Sensing).

Perhaps the best example in Australia was the recognition of Gosses Bluff in the Northern Territory as an impact structure (Figure 8). In the late 1960s detailed geological mapping of Gosses Bluff by joint US Geological Survey and the then Bureau of Mineral Resources teams established the site as a classic example of the central uplift of a medium sized (24 km diameter) complex impact crater of late Jurassic age (Milton *et al.* 1972). The evidence for impact at Gosses Bluff includes impact melts, shatter cones, and shocked quartz. The study involved several Australians, notably Robin Brett (USGS) and Andrew Y Glikson (then at the BMR).

In the 1980s, Eugene Merle (Gene) Shoemaker (1928–1997) an American geologist, and his wife Carolyn Shoemaker, an astronomer, obtained funding to undertake a comprehensive study of impact structures in Australia. In collaboration with Australians, such as Andrew Glikson, the Shoemaker's discovered several new impact sites, and through meticulous mapping improved our knowledge of many of the structures that were already known (Shoemaker & Shoemaker 1996; Shoemaker et al. 2005).

From the early 1980s, an Australian geologist, Peter W Haines (now at the Geological Survey of Western Australia), has discovered and described several new impact structures and remains an active worker in the field. Haines is one of Australia's most prominent impact

specialists and has reviewed the Australian crater record (Haines 2005 and references therein).

Today there are 37 structures in Australia that are recognised to varying degrees of certainty as impact structures. Five of these are small, young, simple bowlshaped craters associated with meteorites (Bevan 1996; Bevan & McNamara 2009). Another 12 possible impact sites are currently under investigation, but to date lack conclusive evidence of an impact origin.

SUMMARY

In Australia, since the late 1880s, contributions to meteoritics and planetary materials have been significant, diverse, and multidisciplinary, including the study of meteorites themselves, lunar rocks and impact cratering. These studies have involved the disciplines of petrology, mineralogy, metallurgy, isotopic studies, geochemistry and geochronology. Today there are active groups of scientists at the Australian National University, Curtin University, the University of Western Australia, Monash University, Sydney University, University of New South Wales, and Macquarie University. Research is also carried out on major collections of meteorites that are held at the Australian Museum in Sydney, and the State Museums of Victoria, South Australia and Western Australia.

ACKNOWLEDGEMENTS

I would like to thank Ross Taylor and Peter Haines for helpful reviews that greatly improved the manuscript.

REFERENCES

- Ahrens L H 1964. Si-Mg fractionation in chondrites. *Geochimica et Cosmochimica Acta* 28, 411–423.
- AHRENS L H 1965. Observations on the Fe-Si-Mg relationship in chondrites. *Geochimica et Cosmochimica Acta* 29, 801–806.
- ALDERMAN A R 1932. The meteorite craters at Henbury, central Australia. *Mineralogical Magazine* 23, 19–32.
- Anderson C 1913. A catalogue and bibliography of Australian Meteorites. Records of the Australian Museum 10, 53–76.
- Benedix G K, McCoy T J, Keil K & Love S G 2000. A petrologic study of the IAB iron meteorites: constraints on the formation of the IAB-Winonaite parent body. *Meteoritics & Planetary Science* 35, 1127–1141.
- Bevan A W R 1992a. Australian meteorites. Records of the Australian Museum Supplement 15, I-27.
- Bevan A W R 1992b. 1992 WAMET/EUROMET joint expedition to search for meteorites in the Nullarbor Region, Western Australia. *Meteoritics* 27, 202–203.
- Bevan A W R 1996. Australian crater-forming meteorites. AGSO Journal of Australian Geology & Geophysics 16, 421–429.
- Bevan A W R 2006. The Western Australian Museum meteorite collection. *In:* McCall G J H, Bowden A J & Howarth R J (eds) *The history of meteoritics and key meteorite collections: fireballs falls and finds,* pp. 305–323. Geological Society of London Special Publication 256.
- BEVAN A W R & BINNS R A 1989a. Meteorites from the Nullarbor Region, Western Australia: I. A review of past recoveries and a procedure for naming new finds. *Meteoritics* 24, 127–133.
- Bevan A W R & Binns R A 1989b. Meteorites from the Nullarbor Region, Western Australia: II. Recovery and classification of 34 new meteorite finds from the Mundrabilla, Forrest, Reid and Deakin areas. *Meteoritics* 24, 134–141.
- BEVAN A W R & BINNS R A 1989c. Further meteorite recoveries from the Nullarbor Region, Western Australia. Meteoritics 24, 251.
- Bevan A W R, Bland P A & Jull A J T 1998. Meteorite flux on the Nullarbor, Australia. *Iu:* Grady M M, Hutchison R, McCall G J H & Rothery D A (eds) *Meteorites: flux with time* and impact effects, pp. 59–73. Geological Society of London Special Publication 140.
- Bevan A W R & McNamara K J 2009. Australia's meteorite craters. Western Australian Museum, Perth.
- BINNS R A 1967a. Structure and evolution of non-carbonaceous chondritic meteorites. *Earth and Planetary Science Letters* 2, 23–28.
- BINNS R A 1967b. Olivine in enstatite chondrites. *Americau Mineralogist* 52, 1549–1554.
- Binns R A 1970. Pyroxenes from non-carbonaceous chondritic meteorites. *Mineralogical Magazine* 37, 649–669.
- BINNS R A, DAVIS R J & REED S J B 1969. Ringwoodite, natural (Mg,Fe)₂SiO₄ spinel in the Tenham meteorite. *Nature* **221**, 943–944.
- BLAND P A, BEVAN A W R & JULL A J T 2000. Ancient meteorite finds and the Earth's surface environment. Quaternary Research 53,131–142.
- BLAND P A, SPURNY P, TOWNER M C, BEVAN A W R, SINGLETON A, BOTTKE W F JR, GREENWOOD R C, CHESLEY S R, SHRBENY L, BOROVICKA J, CEPLECHA Z, McCLAFFERTY T P, VAUGHAN D, BENEDIX G K, DEACON G, HOWARD K T, FRANCHI I A & HOUGH R M 2009. An anomalous basaltic meteorite from the Innermost Main Belt. Science 325, 1525–1527.

- Bland P A, Spurny P, Bevan A W R, Howard K T, Towner M C, Benedix G K, Greenwood R C, Shrbeny L, Franchi I A, Deacon G, Borovicka J, Ceplecha Z, Vaughan D & Hough R M 2012. The Australian Desert Fireball Network: a new era for planetary science. Australian Journal of Earth Sciences 59, 177—187.
- Bowden A J 2006. Meteorite provenance and the asteroid connection. *In*: McCall G J H, Bowden A J & Howarth R J (eds) *The history of meteoritics and key meteorite collections; fireballs, falls and finds,* pp. 379–403. Geological Society of London Special Publication 256.
- Bowler J M 1978. Glacial age aeolian events at high and low latitudes: a southern hemisphere perspective. *In*: Van Zinderen Bakker E M (ed.) *Autarctic glacial history and world palaeoeuvironments*, pp. 149–172. Balkema, Rotterdam.
- Bowler J M, Hope G S, Jennings J N, Singh G & Walker D 1976. Late Quaternary climates of Australia and New Guinea. Quaternary Research 6, 359–394.
- Brenthall W D & Axon H J 1962. The response of Canyon Diablo meteorite to heat treatment. *Journal of the Iron and Steel Institute* 200, 947–955.
- Brett R 1967. Cohenite: its occurrence and proposed origin. Geochimica et Cosmochimica Acta 31, 148–159.
- Brush S G 2006. Meteorites and the origin of the Solar System, In: McCall G J H, Bowden A J & Howarth R J (eds) The history of meteoritics and key meteorite collections; fireballs falls and finds, pp. 417–441. Geological Society of London Special Publication 256.
- Buchwald V F 1975. *Handbook of iron meteorites*, University of California Press, Berkeley.
- Bunch T E, Keil K & Olsen E 1970. Mineralogy and petrology of silicate inclusions in iron meteorites. *Contributions to Mineralogy and Petrology* 25, 297–240.
- Burbidge E M, Burbidge G R, Fowler W A & Hoyle F 1957. Synthesis of the elements in stars. *Reviews of Modern Physics* 29, 547–650.
- CAMERON A G W 1957. Stellar evolution, nuclear astrophysics and nucleogenesis. Chalk River Report, Atomic Energy of Canada Limited CRL-41.
- CLEVERLY W H 1993. The role of the Western Australian School of Mines in meteorite recovery and research. Western Australian School of Mines Annual Magazine 90 years, pp. 59-65.
- COOKSEY T 1897. The Nocoleche meteorite with a catalogue and bibliography of Australian meteorites. *Records of the Australian Museum* 3, 51–62.
- Compston W, Chappell B W, Arriens P A & Vernon M J 1970. The chemistry and age of Apollo 11 lunar material. Proceedings of the Apollo 11 Lunar Science Conference, 1007–1027.
- COMPSTON W & PIDGEON R T 1986. Jack Hills, evidence of more very old detrital zircons in Western Australia. Nature 321, 766–769.
- De Laeter J R & Bevan A W R 1992. A history of Western Australian Meteoritics. *Records of the Western Australian Museum* 15, 749–762.
- De Laeter J R & Jeffery P M 1965. The isotopic composition of terrestrial and meteoritic tin. *Journal of Geophysical Research* 70, 2895–2903.
- Dodd R T 1969. Metamorphism of the ordinary chondrites: a review. *Geochimica et Cosmochimica Acta* 33, 161–203.
- Dodd R T & Van Schmus W R 1965. Significance of the unequilibrated ordinary chondrites. *Journal of Geophysical Research* 70, 3801–3811.
- EDWARDS A B & BAKER G 1944. The Cranbourne meteorites. Memoirs of the National Museum of Victoria 44, 23–35.
- FOSTER J 2010. The construction and development of SHRIMP I: an historical outline. *Precambrian Research* 183, 1–8.
- FREDRICKSSON K & RINGWOOD A E 1963. Origin of meteoritic chondrules. *Geochimica et Cosmochimica Acta* 27, 639–642.

- Frost M J 1965. Kamacite bandwidth estimation in octahedrites. Mineralogical Magazine 35, 640–642.
- Froude D O, Ireland T R, Kinny P D, Williams I S, Compston W, Williams I R & Myers J S 1983. lon microprobe identification of 4,100-4,200 Myr-old terrestrial zircons. *Nature* 304, 616–618
- Gibbons G S 1977. Index of Australian Meteorites. *Journal of the Geological Society of Australia* 24, 263–268.
- GLOVER J 2003. Geological journeys: from artifacts to zircon. Geological Society of Australia, Western Australian Division, Perth.
- Goede A, Harmon R S, Atkinson T C & Rowe P J 1990. Pleistocene climatic change in southern Australia and its effects on speleothem deposition in some Nullarbor caves. *Journal of Quaternary Science* 5, 29–38.
- GOLDBERG E, UCHIYAMA A & BROWN H 1951. The distribution of nickel, cobalt, gallium, palladium and gold in iron meteorites. *Geochimica et Cosmochimica Acta* 2, 1–25.
- GOLDSTEIN J I, SCOTT E R D & CHABOT N L 2009. Iron meteorites: crystallization, thermal history, parent bodies, and origin. Chemie der Erde 69, 293–325.
- Grady M M 2000. Catalogue of meteorites (5th edition). Cambridge University Press, Cambridge.
- Graham A L, Bevan A W R & Hutchison R 1985. Catalogue of meteorites, with special reference to those represented in the collection of the British Museum (Natural History) (4th edition, revised and enlarged). British Museum (Natural History), London & University of Arizona Press, Tucson.
- GRAY C M & COMPSTON W 1974. Excess ²⁶Mg in the Allende meteorite. Nature 251, 495–497.
- Guppy J D & Matheson R S 1950. Wolf Creek Crater. *Journal of Geology* 58, 30–36.
- HAINES P W 2005. Impact cratering and distal ejecta: the Australian record. In: Glikson A Y & Haines P W (eds) Shoemaker Memorial Issue on the Australian impact record: 1997–2005 update, pp. 481–507. Australian Journal of Earth Sciences 52.
- HEY M H 1966. Catalogue of meteorites, with special reference to those represented in the collection of the British Museum (3rd edition, revised, and enlarged). British Museum (Natural History), London.
- HODGE-SMITH T 1939. Australian meteorites. Memoirs of the Australian Museum 7, 1–84.
- HUTCHISON R 2004. Meteorites: a petrologic, chemical and isotopic synthesis. Cambridge University Press, Cambridge.
- Jarosewich E 1990. Chemical analyses of meteorites: a compilation of stony and iron meteorite analyses. *Meteoritics* **25**, 323–337.
- JENNISKENS P, SHADDAD M H, NUMAN D, ELSIR S, KUDODA A M, ZOLENSKY M E, LE L, ROBINSON G A, FRIEDRICH J M, RUMBLE D, STEELE A, CHESLEY S R, FITZSIMMONS A, DUDDY S, HSIEH H H, RAMISAY G, BROWN P G, EDWARDS W N, TAGLIAFERRI E, BOSLOUGH M B, SPALDING R E, DANTOWITZ R, KOZUBAL M, PRAVEC P, BOROVIĆKA J, CHARVAT Z, VAUBAILLON J, KUIPER J, ALBERS J, BISHOP J L, MANCINELLI R L, SANDFORD S A, MILAM S N, NUEVO M & WORDEN S P 2009. The impact and recovery of asteroid 2008 TC₃. Nature 458, 485–488.
- JULL A J T 2006. Terrestrial ages of meteorites. In: Lauretta D S & McSween H Y (eds) Meteorites and the early Solar System II, pp. 889–905. University of Arizona Press, Tucson.
- KELLY W R & LARIMER J W 1977. Chemical fractionations in meteorites. VIII — Iron meteorites and the cosmochemical history of the metal phase. Geochimica et Cosmochimica Acta 41, 93–111.
- Kracher A, Willis J & Wasson J T 1980. Chemical classification of iron meteorites—IX. A new group (IIF), revision of IAB and IIICD, and data on 57 additional irons. *Geochimica et Cosmochimica Acta* 44, 773–787.
- LEE T, PAPANASTASSIOU D A & WASSERBURG G J 1976.

- Demonstration of ²⁶Mg excess in Allende and evidence for ²⁶Al. *Geophysical Research Letters* 3, 109–112.
- LIVERSIDGE A 1872. The Deniliquin or Barratta meteorite. Proceedings of the Royal Society of New South Wales 6, 97–103.
- LOVERING J F 1957. Differentiation in the iron-nickel core of a parent meteorite body. *Geochimica et Cosmochimica Acta* 12, 238–252.
- LOVERING J F, NICHIPORUK W, CHODOS A & BROWN H 1957. The distribution of gallium, germanium, cobalt, chromium and copper in iron and stony-iron meteorites in relation to nickel content and structure. Geochimica et Cosmochimica Acta 11, 263–278.
- LOVERING J F, WARK D A, GLEADOW A J W & BRITTEN R 1974. Lunar monazite: a late-stage (mesostasis) phase in mare basalt. Earth and Planetary Sciences Letters 21, 164–168.
- LOVERING J F, WARK D A, REID A F, WARE N G, KEIL K, PRINZ M, BUNCH T E, EL GORESY A, RAMDOHR P, BROWN G M, PECKETT A, PHILLIPS R, CAMERON E N, DOUGLAS J A V & PLANT A G 1971. Tranquillityite: a new silicate mineral from Apollo 11 and Apollo 12 basaltic rocks. Proceedings of the 2nd Lunar Science Conference, 39–45.
- MACPHERSON G J 2005. Calcium-aluminium-rich inclusions in chondritic meteorites. In: Davis A M (ed.) Meteorites, comets and planets (Treatise on Geochemistry 1), pp. 201–246. Elsevier-Pergamon, Oxford.
- MacPherson G J, Wark D A & Armstrong A 1988. Primitive material surviving in chondrites: Refractory inclusions. *In:* Kerridge J & Matthews M S (eds) *Meteorites and the early Solar System,* pp. 746–807. University of Arizona Press, Tucson.
- MADIGAN C T 1937. The Box Hole crater and the Huckitta meteorite (central Australia). Transactions of the Royal Society of South Australia 61, 187–190.
- MARTIN H A 1973. Palynology and historical ecology of some cave excavations in the Australian Nullarbor. *Australian Journal of Botany* 21, 283–316.
- MARTIN P M & MASON B 1974. Major and trace elements in the Allende meteorite. *Nature* 249, 333–334.
- MASON B 1962. Meteorites. Wiley, New York.
- Mason B 1974. Notes on Australian meteorites. Records of the Australian Museum 29, 169–186.
- Mason B & Martin P M 1977. Geochemical differences among components of the Allende meteorite. Smithsonian Contributions to Earth Sciences 19, 84–95.
- MASON B & TAYLOR S R 1982. Inclusions in the Allende meteorite. Smithsonian Contributions to Earth Sciences 25, 1–30.
- McCall G J H 1966. Dalgety Downs chondritic meteorite. Journal of the Royal Society of Western Australia 49, 52–58.
- McKeegan K D & Davis A M 2005. Early Solar System chronology. In: Davis A M (ed.) Meteorites, comets and planets (Treatise on Geochemistry 1), pp. 431–460. Elsevier-Pergamon, Oxford.
- MILTON D J, BARLOW B C, BRETT R, BROWN A R, GLIKSON A Y, MANWARING E A, MOSS F J, SEDMIK E C E, VAN SON J & YOUNG G A. 1972. Gosses Bluff impact structure, Australia. *Science* 175, 1199–1207.
- NARAYAN C & GOLDSTEIN J I 1982. A dendritic solidification model to explain Ge-Ni variations in iron meteorite chemical groups. *Geochimica et Cosmochimica Acta* 46, 259–268.
- Price G D, Putnis A, Agrell S O & Smith D G W 1983. Wadsleyite, natural β-(Mg,Fe), SiO₄ from the Peace River meteorite. *Canadian Mineralogist* 21, 29–35.
- PRIOR G T 1916. On the genetic relationship and classification of meteorites. Mineralogical Magazine 18, 26–44.
- PRIOR G T 1920. The classification of meteorites. Mineralogical Magazine 19, 51–63.
- PRIOR G T 1923. Catalogue of Meteorites, with special reference to those represented in the collection of the British Museum (Natural History). British Museum (Natural History), London.

- Prior G T & Hey M H 1953. Catalogue of Meteorites, with special reference to those represented in the collection of the British Mnseum (Natural History) (2nd edition). British Museum (Natural History), London.
- RAMDOHR P 1967. Observations on the opaque ore content of some meteorites, especially from New South Wales. *Journal and Proceedings of the Royal Society of New South Wales* 99, 45–55.
- RASMUSSEN B, FLETCHER 1, GREGORY C J, MUHLING J R & SUVOROVA A A 2011. Tranquillityite: the last lunar mineral comes down to Earth. *Geology* 40, 83–86.
- Reeves F & Chalmers R O 1949. The Wolf Creek Crater. Australian Journal of Science 11, 145-156.
- REYNOLDS J H 1960. Isotopic composition of primordial xenon. *Physics Review Letters* 4, 351–354.
- RINGWOOD A E 1959. On the chemical evolution and densities of the planets. *Geochimica et Cosmochimica Acta* 15, 257–287.
- RINGWOOD A E 1961. Chemical and genetic relationships among meteorites. *Geochimica et Cosmochimica Acta* 24, 159–197.
- RINGWOOD A E 1962. Present status of the chondritic Earth model. In: Moore C B (ed.) Researches on meteorites, pp. 198– 216. John Wiley & Sons, New York.
- Ringwood A E 1966. Genesis of chondritic meteorites. *Reviews in Geophysics* 4, 113–175.
- RINGWOOD A E & MAJOR A 1966. Synthesis of Mg₂SiO₄-Fe₂SiO₄ spinel solid solutions. *Earth and Planetary Science Letters* 1, 241–245.
- RINGWOOD A E & MAJOR A 1971. A synthesis of majorite and other high pressure garnets and perovskites. *Earth and Planetary Science Letters* 12, 411–418.
- RINGWOOD A E & SEABROOK M P 1962. Collenite as a pressure indicator in iron meteorites II. *Geochimica et Cosmochimca Acta* 26, 507–509.
- Rubin A E 1997a. Mineralogy of meteorite groups. *Meteoritics & Planetary Science* **32**, 231–247.
- Rubin A E 1997b. Mineralogy of meteorite groups: an update. Meteoritics & Planetary Science 32, 733–734.
- Rubin A E 2000. Petrologic, geochemical and experimental constraints on models of chondrule formation. *Earth-Science Reviews* 50, 3–27.
- Schmitt R A, Smith R H & Goles G G 1966. Chainpur-like chondrules: primitive precursors of ordinary chondrites. *Science* 153, 644–647.
- Schramm D N, Tera F & Wasserburg G J 1970. The isotopic abundance of ²⁶Mg and limits on ²⁶Al in the early solar system. *Earth and Planetary Science Letters* **10**, 44–59.
- Scott E R D 1972. Chemical fractionation in iron meteorites and its interpretation. *Geochimica et Cosmochimica Acta* 36, 1205–1236.
- Scott E R D 1977. Composition, mineralogy and origin of group IC iron meteorites. *Earth and Planetary Science Letters* **37**, 273–284.
- Scott E R D 1979. Origin of anomalous iron meteorites. *Mineralogical Magazine* 43, 415–421.
- Scott E R D & Wasson J T 1975. Classification and properties of iron meteorites. *Reviews in Geophysics and Space Science* 13, 527–546.
- Scott E R D & Wasson J T 1976. Chemical classification of iron meteorites—VIII. Groups 1C, 1IE, IIF and 97 other irons. Geochimica et Cosmochimica Acta 40, 103–115.
- SHOEMAKER E M, MACDONALD F A & SHOEMAKER C S 2005. Geology of five small Australian impact craters. In: Glikson A Y & Haines P W (eds) Shoemaker Memorial Issue on the Australian impact record: 1997–2005 update, pp. 529–544. Australian Journal of Earth Sciences 52.

- Shoemaker E M & Shoemaker C S 1996. The Proterozoic impact record of Australia. AGSO Journal of Australian Geology & Geophysics 16, 379–398.
- Shu F H, Shang H, Gounelle M, Glassold A E & Lee T 2001. The origin of chondrules and refractory inclusions in chondritic meteorites. *Astrophysics Journal* 548, 1029–1050.
- SIMPSON S 1938. Some new and little-known meteorites found in Western Australia. *Mineralogical Magazine* 25, 157–171.
- Smith J V & Mason B 1970. Pyroxene-garnet transformation in Coorara meteorite. *Science* 168, 832–833.
- Spurny P, Bland P, Shrbeny L, Towner M, Borovicka J & Beyana 2011. The Mason Gully meteorite fall in SW Australia: fireball trajectory and orbit from photographic records. *Meteoritics & Planetary Science* 46 abstract 5101 (74th Annual Meeting of the Meteoritical Society)
- STREET F A & GROVE A T 1979. Global maps of lake-level fluctuations since 30,000 yr BP. Quaternary Research 12, 83–118.
- Sutton P 2012. Paul Ramdohr in Australia: contributions to mineralogy, mineragraphy, ore genesis and meteoritics resulting from his three visits. *Historical Records of Australian Science* 23, 142–158.
- TAYLOR S R 1973. Tektites: a post Apollo view. Earth-Science Reviews 9, 101–123.
- THOMAS W W & DE LAETER J R 1972. The analysis of nickel, gallium and germanium in iron meteorites by x-ray fluorescence spectrometry. *X-ray Spectrometry* 1, 143–146.
- UREY H C 1952. The planets: their origin and development. Yale University, New Haven.
- UREY H C & CRAIG H 1953. The composition of stone meteorites and the origin of the meteorites. *Geochimica et Cosmochimica Acta* 4, 36–82.
- VAN SCHMUS W R & WOOD J A 1967. A chemical-petrologic classification for the chondritic meteorites. Geochimica et Cosmochimica Acta 31, 747–765.
- Von Haidinger W K 1861. Zwei Meteoreisenmassen in der Nahe von Melbourne in Australien aufgefunden. Sitzingsberichte de Akademie der Wissenschaften Wien 43, 583–584.
- Von Michaelis H, Ahrens L H & Willis J P 1969. The composition of stony meteorites II. The analytical data and an assessment of their quality. *Earth and Planetary Science Letters* 5, 387–394.
- WARK D A 1985. Combined chemical/petrological classification of Ca-Al-rich inclusions. *Proceedings of the 16th Lunar and Planetary Science Conference*, 887–888.
- WARK D A 2005. Recipes for making synthetic CAIs, refractory residues, and minerals for rim-forming experiments. Meteorities & Planetary Science 40, 711–720.
- WARK D A & BOYNTON W V 2001. The formation of rims on Ca-Al-rich inclusions: Srep I Flash heating. *Meteoritics & Planetary Science* 36, 1135–1166.
- WARK D A & LOVERING J F 1977. Marker events in the early evolution of the solar system: evidence from rims on Ca-Alrich inclusions in carbonaceous chondrites. *Proceedings of the 8th Lunar Science Conference*, 95–112.
- WARK D A & LOVERING J F 1980. Second thoughts about rims. Proceedings of the 11th Lunar and Planetary Science Conference, 1211–1213.
- WARK D A, REID A F, LOVERING J F & EL GORESY A 1973.
 Zirconolite (versus Zirkelite) in lunar rocks. Proceedings of the 4th Lunar Science Conference, 764–766.

Received 4 January 2014; accepted 12 March 2014

Advances in mathematics and statistics in Western Australia since 1960

A P BASSOM*, J HOPWOOD, J L NOAKES, A G PAKES & C E PRAEGER

School of Mathematics & Statistics, University of Western Australia, 35 Stirling Highway, Crawley WA 6009 * Corresponding author 🖾 andrew.bassom@uwa.edn.au

We review some of the key developments in mathematics and statistics over the last half-century concerning researchers either based in, or originating from, Western Australia. We describe the whole range of mathematical sciences from the work in the most abstract and theoretical aspects of pure mathematics through to the most applied area of statistics.

KEYWORDS: applied mathematics, mathematics, mathematical science, pure mathematics, statistics, Western Australia.

INTRODUCTION

It was with more than a little trepidation that we accepted this task of penning a short article on some of the significant advances that have occurred within Mathematics and Statistics by researchers based in our state. Even though our timeframe extends over only roughly a 50 year period, this time has seen some dramatic changes in the mathematical landscape, prompted in part by the sea change that has taken place in computational capability. As a demonstration of this revolution, it should be noted that the first computer installed in the University of Western Australia (UWA) in the early 1960s occupied a large room and had a computational power far less than is in a hand-held calculator now used routinely in a high-school classroom.

Any account such as this can only touch on a few of the key developments within a particular field of science and must by necessity be extremely selective. The responsibility for the choice of subject matter rests solely with the authors who apologise for any glaring omissions. Moreover, since all the writers of this article are based at UWA, there is the clear danger that the overall focus of our account becomes rather UWA-centric—we hope that we have avoided falling into this trap. We mention that there are several seminal reviews of mathematics and statistics in the whole of Australia; of these perhaps the most comprehensive is Cohen (2006) and further details and many references can be found there.

Before any attempt to describe some of the advances that have taken place in the mathematical sciences it is perhaps helpful to outline exactly what mathematical science is in the modern research setting. (In what follows we will occasionally mention mathematical science as a generic term by which we mean mathematics and statistics combined – a phrase that can become cumbersome if often repeated.) Mathematical science is conveniently divided into three subclasses, which we shall refer to as pure mathematics, applied mathematics and statistics. Broadly speaking pure mathematics is the branch that studies entirely abstract concepts; it is possible to study such constructs with respect to their intrinsic properties without need for any application to

the real world. On the other hand, applied mathematics is concerned with methods that can be used in a variety of problems that may occur in science, engineering or industry. Last, but by no means least, statistics is the study of collection, organisation, analysis and interpretation of data. The boundaries between these separate branches of mathematics are somewhat blurred - indeed it is difficult to define exactly where studies in some topics, especially within applied mathematics and statistics, morph into other disciplines like physics, computer science or medicine. Mathematical links with computer science are especially strong; for instance the present Deputy Vice Chancellor (Research) at UWA, Robyn Owens, was for some years Professor of Computer Science following on from a PhD in mathematics at Oxford. In order to keep the scope of this article manageable we deliberately focus on activities of workers based in mathematics departments and, to help the reader identify our references to the separate subdisciplines in what follows, Table 1 sets out how some key personnel fit into the overall picture.

It is important to emphasise that the landscape of the mathematical sciences has evolved markedly over the last half century. Researchers in the field back in the 1960s would not recognise some of the contexts in which mathematics now plays an integral part. The advent of fast digital computers has revolutionised the way in which mathematical research is conducted in all three branches. Whole new fields of mathematics applied to biology and to finance have opened up, while statistics plays a significant role in many parts of health and medical research. Thus modern mathematical developments now occur in a far wider setting than just within the rather traditional university department. Much mathematical work is undertaken in government organisations like CSIRO, within hospitals, or research arms of commercial companies and there are numerous pockets of other activity scattered widely. It would be an impossible task for us to even begin to try to compile an account of all the significant mathematical work done outside universities and we have not endeavoured to do this. Thus our remarks will concentrate on research emanating from Western Australian universities, but acknowledge that this cannot be a comprehensive account of all work that has been conducted in the state over the past 50 years.

Table 1 Some professorial appointments in mathematics and statistics in Western Australian universities together with significant milestones that have occurred since 1960.

Year	Curtin University	Murdoch University	University of Western Australia			Some significant events		
			Applied	Pure	Statistics	CVCIII		
Pre-1960	-	-	Weatherburn (to 1952)	Blakers (to 1982)	-	-		
1960-1965			Levey (1961-66) Mahony (1964-86)	-		Summer courses for school students		
1966-1970		-		Silberstein (1966-85)		-		
1971-1975	-	Robertso n (1973-90)			-	Murdoch starts		
1976-1980	• .			-	Speed (1976-82)	UWA Statistical Consulting Group Math. Olympiad Committee		
1981-1985			Mees (1984-2002)	Praeger (1983-)	Brown (1987-92)	MISG		
1986-1990		-		-	-	WAIT becomes Curtin		
1991-1995	Caccetta (1992-)	James (1991-) Bloom (1995-2011)		-	Aitkin (1994-97) Baddeley (1994-2010)	ECU Mathematics Problem Solving Program (1991-) UWA Academy of Young Mathematicians (1995-)		
1996-2000	Teo (1997-99)		-		-	CADO (1996-2005) WAJO		
2001-2005	Teo (2005-)		Bassom (2005-)	Noakes (2005-)	Gao (2004-07)	WACEIO formed at Curtin		
2006-2010	Wu (2008-)	-	-		-	CMSC formed at UWA		
2011-	Wang (2014-)	Hocking (2011-)	Small (2012-)	Seress (2011-12) Li (2013-)		-		

1960s AND 1970s

Half-a-century ago the mathematical scene in Western Australia was very different from its relative vibrancy of today. The little research that was being conducted was based at UWA, being the only university in Perth at the time. Staff in mathematics had an almost entirely teaching role and much of their time was spent educating other scientists and engineers in the mathematical methods required for the study of their particular subjects. Significant progress in the research capabilities of the state was achieved by the appointment of Harry Levey to a Professorship in Applied Mathematics in 1962. He came to Perth from the ARL (the Aeronautical Research Laboratories which at the time was a division of the CSIRO). Others subsequently also made the transition along the same route and thereby a nucleus of research activity in applied mathematics evolved. Levey himself enjoyed an international reputation in fluid dynamics, and particularly in gas dynamics (see Mahony 1968) and these subjects occupied a prominent position in the research direction at that time while studies of

electromagnetic theory and astrophysics were also undertaken.

The day-to-day nature of work in those early days would be almost unrecognisable to the mathematicians currently engaged in research. In those days, of course long before the birth of email and the internet, there was great emphasis placed in maintaining personal research connections. UWA had particularly strong links with staff at the University of Queensland and with several overseas institutions. In this era even making national and international telephone calls was far from easy and so personal visits of one researcher to another played a very important part in the intellectual life of the university and the state. Western Australia hosted some very eminent workers from overseas. We mention just one, George Batchelor, a world expert in fluid mechanics who was an expatriate from Victoria and eventually become Head of the Department of Applied Mathematics and Theoretical Physics at Cambridge University.

Unfortunately Levey's tenure in UWA was short-lived and he died suddenly during 1966. Slightly earlier a

second Chair in Applied Mathematics had been taken up by John Mahony, who had been a colleague of his at the ARL. The middle-to-late 1960s marked a particularly active period and the main research focus was in the field of continuum mechanics (which essentially is concerned with a mathematical description of the properties of solids and fluids). Several more people joined the group including Neville Fowkes who is still a member of staff in the UWA School of Mathematics and Statistics today. Neville was not only a wonderful mathematician but a fearsome competitor on the tennis and squash courts - he holds the distinction of having beaten Rod Laver in a Queensland boys singles final in the mid 1950s. Under the guidance of Fowkes and Mahony the principal research direction of the group shifted to look at a collection of problems classified as being of singular perturbation type. Loosely speaking, singular perturbation problems are characterised by the property that seemingly small terms in equations, which therefore intuitively ought to be in some sense negligible, turn out to play an integral part in fixing the solution. As an example, fluid friction (termed viscosity) is tiny when calculating the flow of air over an aircraft wing but it is central in determining the drag exerted by the flow on the body. Mahony tackled these types of problems by developing a method now universally referred to as multi-scaling (or two-timing) and which is now a standard method in a plethora of research fields. Further work was directed to understanding the properties of gravity waves and the dynamics of water in reservoirs. Jorg Imberger, who joined the department first as a postgraduate student and later as a staff member, had particular interest in this class of problems. Jorg subsequently became director of the world-renowned Centre for Water Research based at UWA.

By 1970 the academic members of the mathematics group numbered about 15, headed by A L (Larry) Blakers, who was appointed professor on the retirement of the Foundation Professor of Mathematics Charles Weatherburn in 1952. (We remark that Weatherburn inspired a nursery-age book written many years later: see Magain 2011.) Larry's initiatives in the 1950s included being one of the players in the establishment of the Australian Mathematical Society in 1956 (for more details see Cohen 2006). He was also prominent in the formation of the Mathematical Association of Western Australia (MAWA) in 1958 (Blakers 1979) and his drive also established the Australian Association of Mathematics Teachers in 1966 (Gani 2001). Under Larry's leadership there was a dramatic growth in mathematics personnel although there was no Professor of Statistics at UWA until 1976. Rather, research and teaching in that area relied on a variety of short-term senior appointments and a small kernel of more junior staff. Joe Gani had been appointed in the late 1950s to develop statistics but he left in 1960 to pursue a very distinguished career both overseas and elsewhere in Australia. His research area is now known as applied probability, which is concerned with how probability theory can be used to solve practical problems. Gani's focus was in bacteriophages, dams and epidemics. One of his students, N U Prabhu, was a staff member from 1962 until 1965 and worked in the fluctuation theory of queuing systems and wrote two distinguished monographs; one was arguably the earliest text on the

subject directed at the advanced undergraduate or graduate student level while the other, that is still cited today, proved to be regarded as one of the best treatments of the subject. These pioneers established a continuing tradition of applied probability at UWA with a whole succession of researchers who went on to become professors at various institutions around the world.

Mention should be made of K Vijayan who was appointed a visiting lecturer in 1967 and returned as a senior lecturer in 1969 when he became the first long-term appointment in statistics. His principal research interests were in the apparently disparate fields of the sampling of finite populations and in the pure mathematics area of combinatorial design theory. Vijayan retired at the end of 2007 and has the unique distinction in Western Australia of being the only mathematician with an Erdős number of one 1. His most successful PhD student is Lou Caccetta, who is the current Head of Mathematics at Curtin University and Director of the Western Australian Centre of Excellence in Industrial Optimisation (WACEIO) which was founded in 2001. Lou's research interests are primarily in the field of graph theory and its applications in the design and analysis of networks, especially in the context of vehicle routing problems, openpit mining and network reliability.

A significant development occurred with the appointment in 1974 of Terry Speed who was promoted to Professor of Statistics in 1976. Terry brought immense energy and talent to UWA and although his background was in algebra and probability theory, he soon perceived the need for high-level statistical advice. Consequently he set about retraining himself as both a theoretical and applied statistician and actively sought opportunities to find challenging problems that were amenable to statistical analysis. He contributed to the enquiries into Aboriginal deaths in custody, asbestos exposure and mesothelioma. Terry founded the embryo UWA Statistical Consulting Group whose ongoing viability was assured by substantial grants received from the Domestic Water Use Study (DWUS, 1979-84) sponsored by the Metropolitan Water Authority. One of the most extensive such studies, it involved scientific staff from the CSIRO Division of Groundwater Research and the Australian Bureau of Statistics. The Consulting Group was responsible for the storage, processing and analysis of the enormous quantity of data generated by the survey and this required the appointment of several new staff in statistics. Terry's work also involved insightful investigations of the algebraic structures inherent in the analysis of variance and contingency tables. He examined the models coded into Genstat and GLIM that were at the time the two most important statistical computing packages. Terry attracted many high-profile visitors from all over the world and he left UWA at the end of 1982 to take up the position of the Chief of the CSIRO Division of Mathematics and Statistics. One

¹ Paul Erdős (1913–1996) published more papers (over 1500) than any other mathematician. The Erdős number was invented as an informal measure of mathematical prominence. If an individual coauthored a paper with Erdős his number is one; anyone who has written a paper with someone with Erdős number one then has a Erdős number of two and so on. Vijayan is one of only 509 people with an Erdős number 1.

measure of Terry's achievements is the fact that he was elected a Fellow of the Royal Society of London – the oldest and arguably most prestigious scientific society in the world – in between the drafting and revision of this paper; and was awarded the 2013 Prime Minister's Prize for Science in recognition of his contributions to genomics and related technologies, just before this paper went to proof.

One notable appointee in statistics at UWA was Richard Tweedie, who was interested in theoretical aspects of probability. His subsequent very distinguished career included Foundation Dean at Bond University, Professor and Chair of Statistics at Colorado State University and, finally, at the University of Minnesota. The significance of his work is commemorated by the annual Tweedie New Researcher Award presented by the Institute of Mathematical Statistics².

The 1970s also saw the emergence of a mathematics department at Murdoch University. In 1963 Larry Blakers was looking for an algebraist to teach at UWA and was recommended to approach a functional analyst (another branch of pure mathematics), Alex Robertson, who was at Glasgow University. Unfortunately he was unable to come to Perth on that occasion but did come (along with his wife Wendy, also a mathematician) as Visiting Professor at UWA in 1969. Subsequently he was appointed Foundation Professor of Mathematics at Murdoch in 1973, 18 months before Murdoch accepted its first students. Alex played a key part in the formation of Murdoch - a role he fulfilled right through to his retirement in 1990. Alex recruited and retained an impressive team of younger mathematicians, many of whom are still active at the University today and to whom the high esteem of the current mathematics degree program at Murdoch can be ascribed. Alex and Wendy Robertson are well known for their book, Topological Vector Spaces, used as an advanced text throughout the world, especially in Europe, in its original version and also its German and Russian translations. Wendy Robertson joined the group of pure mathematicians at UWA headed by J P O (Phil) Silberstein, who was appointed professor in 1966. Phil had come to UWA in 1960 from ARL where he had worked on mathematical problems associated with several applications such as the directional stability of aircraft. The flourishing groups of pure mathematicians at Murdoch and UWA established a joint weekly seminar that ran for more than a decade, meeting alternately at each institution. This facilitated active research collaborations, for example, between Ken Harrison (Murdoch) and Bill Longstaff (UWA) working on the theory of subspace lattices. A member of this seminar, Lyn Bloom, later joined the staff of Edith Cowan University where she, together with David McDougall and Ute Muller, developed a successful programme in geostatistics, which trains undergraduate and postgraduate students in the theory and methods for applying statistics and mathematical modelling to the analysis of data arising in the earth and environmental

sciences—of particular relevance to the mining, environmental and petroleum industries.

The mid 1970s also saw the appointments of Lyle Noakes and Cheryl Praeger to UWA. During this period George Wilson worked at UWA on problems in algebraic geometry, especially investigations into Hilbert's Sixteenth Problem³. George's subsequent work at Oxford included collaboration with Graeme Segal (another distinguished Australian mathematician).

1980s AND 1990s

Apart from conducting original research, one of the most important functions of any body of academics is to train and encourage the young minds of today to flourish and become the subject leaders in their generation. This is a task that has always been taken seriously in Western Australia and significant work in mathematical enrichment and challenge activities began back in the 1960s. Larry Blakers was fully supportive of his staff who wanted to be involved in this type of activity and he was instrumental in setting up both the Western Australian Schools Mathematics Enrichment Course based at UWA and the National Mathematics Summer School at the Australian National University (ANU), both of which were designed for gifted high-school students. Larry was himself the Director of the first 24 national schools and was subsequently awarded an Honorary Doctor of Laws by ANU in 1992 in recognition of his outstanding service. Many UWA staff, as well as teachers associated with MAWA contributed to the Western Australian summer

It is perhaps not widely known but each year there is an international competition between the very best mathematics students of each country in an International Mathematics Olympiad (IMO). Teams of six are entered and undergo a rigorous training schedule to prepare them for the fearsomely difficult problems that they will be challenged with at the IMO. In 1980 Norm Hoffman became the Australian Mathematical Olympiad Committee's first Western Australian state director. Several years later he was succeeded by Phill Schultz who, in turn, was followed by Elena Stoyanova and Greg Gamble. Through these programs some truly exceptional Western Australian high-school students were introduced to problem solving and some have become well-known mathematicians. To name just three, mention should be made of Peter McNamara who was the first Australian to win two gold medals at IMOs; Akshay Venkatesh who is now based at Stanford in California and is widely acknowledged to be one of the world's best mathematicians, and of Andrew Hassell, who is a researcher at ANU and has just been elected a Fellow of the Australian Academy of Science. In 1991 Norm Hoffman commenced a series of after-school classes for able primary and secondary school students and hosted by Edith Cowan University. Each year around 200 students participate in these classes.

² http://www.imstat.org/awards/tweedie.html

³ The German mathematician David Hilbert compiled a list of 23 problems in 1900. Some of these turned out to be very influential in the development of 20th century mathematics and several researchers were awarded Fields medals (the 'Nobel Prize' in Mathematics) for their work on them. To date it is accepted that of the original 23 problems, 10 are solved, 5 remain unresolved and partial solutions have been found for the remainder.

The Western Australian summer schools ceased when UWA was unable to continue funding. However Luchezar Stoyanov and his wife Elena Stoyanova arrived in Perth during 1992. They both had had leading roles in the training of the Bulgarian team at the Olympiads and were keen to see renewed support by the UWA mathematics department for mentoring gifted students. Under their charismatic leadership two new initiatives were born. In 1995 the UWA Academy for Young Mathematicians was started providing Saturday morning mathematics enrichment classes for year 10 and 11 students. Subsequently the Western Australia Mathematics Olympiad Committee initiated the Western Australia Junior Mathematical Olympiad (WAJO), an annual team competition for year 8 and 9 high school students. Prizes for performance in the WAJO are sponsored by each of the four public Western Australian universities, MAWA, as well as bodies connected with the public, catholic and independent school systems together with a number of commercial sponsors.

This era not only saw a dramatic increase in engagement between Western Australian universities and high-school activities but also heralded the widescale entry of computers into both teaching and research at universities. The first computing laboratory for use by undergraduates was opened at UWA in 1992 by Kim Beazley, as his first public act in his then new role as Federal Minister for Education. In conjunction with this new technology, Kevin Judd developed an assessment package called Calmaeth. This system was many years ahead of its time for it has only been relatively recently that companies have been able to market systems that boast of testing capabilities that exceed those of the original Calmaeth. Although some other universities, in particular the University of Adelaide, did use Calmaeth for a number of years it was never made widely available and remained largely in-house. Nevertheless, as a testament to the durability of the package, it is still an integral part of the assessment procedures used for the large first year mathematics classes at UWA.

When Larry Blakers retired in 1982, UWA searched for a professor in 'any area of pure or applied mathematics', since they had flexibility knowing that Phil Silberstein would also retire in two more years. This search resulted in two appointments: pure mathematician Cheryl Praeger, who had joined UWA from ANU as a lecturer in 1976, was appointed to Larry Blakers' Chair in late 1983, and applied mathematician Alistair Mees from Cambridge became Visiting Professor in 1984 until the retirement of Phil Silberstein. Praeger was only the second female mathematician appointed to a Chair at an Australian University, the first being Hanna Neumann at ANU (from 1964 to her death in 1971). She was second also to Hanna as female mathematicians elected as Fellows of the Australian Academy of Science (they were elected in 1969 and 1996 respectively), and was the first woman Head of the UWA Department of Mathematics (1992-1994) and first female President of the Australian Mathematical Society from 1992-1994 (Bhathal 1999). She is still the only mathematician and only woman to become Western Australian Scientist of the Year (2009), and the only woman to win the renowned Thomas Ranken Lyle Medal of the Australian Academy of Science (2013). Praeger built up a worldleading research team of postgraduate students and postdoctoral researchers in Group Theory and Combinatorics. Her first postdoctoral researcher, Tim Penttila, an Australian Research Grants Scheme fellow (1986–1987) and on the regular staff from 1989, built additional research strength in finite geometry, which models properties of geometric figures under projection. Among Penttila's important discoveries at UWA is a family of geometric configurations that he aptly named the *Subiaco ovals* after the famous local football ground.

The 1980s also saw the instigation of the Mathematics in Industry Study Group (MISG). The driving force behind MISG was Noel Barton who was working for CSIRO in Sydney but who had earlier obtained his doctorate from UWA under the supervision of Peter Chapman. The idea of the MISG is to bring together applied mathematicians with workers from various industries to tackle problems that appear to be amenable to mathematical solution. There is a concentrated workshop held somewhere in Australia for a week each January and, as one of the authors can attest, these are great fun. At a recent MISG there were problems associated with the rolling of steel, the efficient spraying of crops with insecticide and the design of the drum of a washing machine to prevent excessive vibration during a high-speed spin cycle. Western Australian mathematicians from UWA, Curtin and Murdoch were active in the MISG from its inception and this has continued to this day. Indeed the MISG has expanded its activities and Western Australian-based mathematicians regularly support the programme at workshops throughout southeast Asia and Africa.

John Mahony was particularly active during the early days of MISG but he had to relinquish his chair of applied mathematics at UWA in 1986 owing to ill-health (Fowkes & Siberstein 1995). His successor Alistair Mees held the post until 2002 when he moved to the United States. Alistair's principal research interests were in the fields of chaos and dynamical systems. These topics were newsworthy at the time, not only within the scientific world but to the general public as well. It was known that biological or physical systems that are deterministic, but inherently unpredictable, might undergo possible dramatic shifts in state. This phenomenon is associated with a structure with a so-called fractional dimension and such structures can be represented by the popular and beautiful abstract patterns known as fractals. There was a very active research group applying the concept of chaotic dynamical systems to problems in medical science, biology, commerce and finance, and climate science. Kevin Judd's interest in atmospheric dynamics led to the development of innovative techniques for dealing with the uncertainties inherent in a chaotic system and he continues to work on these ideas focussed on the topical problem of climate change.

Alistair Mees collaborated with the pure mathematician Lyle Noakes at UWA on recovering dynamical systems from measurements of random variables. Prominent in this area also was Peter Kloeden (Murdoch), who made important contributions to mathematical meteorology. Together with Phil Diamond from the University of Queensland, Peter wrote a highly cited series of papers on fuzzy metric spaces, leading to an influential book on the subject. With Robert Wells (Penn State) he gave the first

explicit example of a Hopf bifurcation in fluid mechanics, and his paper with Jens Lorenz is widely regarded as a milestone in the development of numerical dynamics. Peter moved to Germany in 1997. In 2005 he was awarded the W T and Idalia Reid Prize, a prestigious international award made by the Society for Industrial and Applied Mathematics for fundamental contributions to the theoretical and computational analysis of stochastic differential equations.

The last few years of the twentieth century also saw continued work in mathematical modelling with particular emphasis on problems arising in fluid mechanics. Research in this area was pursued by Graeme Hocking who was then at UWA but is now Head of Mathematics at Murdoch. Other work in applied mathematics included the application of mathematical techniques to attempt to understand medical problems such as epilepsy and studies with members of the Department of Physical Education on human biomechanics that led to significant improvements in the training regimes for athletes. Investigations with geologists on time-series data used the state-of-the-art construct known as wavelet analysis to infer the evolution of the geological structure of key areas of Western Australia. Jo Ward, a UWA graduate, worked on wavelets while based at Murdoch before moving to become Dean of Science at Curtin.

Another major research thread in the area was that of operations research and optimal control, which is concerned with providing engineers and industry with efficient and safe ways of managing large and complex systems. The Centre for Applied Dynamics and Optimisation (CADO) was founded at UWA and Kok-Lay Teo led this group before moving to Curtin in 1997. Teo has published five books and more than 400 journal papers. His software package MISER (developed jointly with C J Goh, Mike Fisher and Les Jennings at UWA) is a fundamental tool for solving constrained optimal control problems. He was also one of six researchers who in 2000 established the Pacific Optimization Research Activity Group, which now has over 500 members from 50 countries. Teo left Curtin in 1999 for a spell in Hong Kong but re-joined in 2005 when he began a period as Head of the Department of Mathematics and Statistics.

We have already mentioned that in the late 1970s Terry Speed founded the UWA Statistical Consulting Group that was supported by the Domestic Water Use Study (DWUS). The group had several members who went on to have very successful careers. lan James was principally interested in the general area of biostatistics that is concerned with the application of statistical methods to biological and medical contexts. In 1991 Ian moved to Murdoch as Professor and Head of the School of Mathematics. He helped found, and is Deputy Director of, the Institute for Immunology and Infectious Diseases at Murdoch and Royal Perth Hospital. His work there concentrates on issues arising from the complex interactions between adaptable pathogens, drugs and the human host at the genetic, cellular and clinical levels. Ian served a term as the Editor of the prestigious Australian Journal of Statistics and he directed the UWA Statistical Consulting Group over most of the period 1982 until 1990. Another member of the Group, Matt Knuiman, conducted further research in medical statistics. After a spell in the

DWUS, followed by four years with the Department of Biostatistics at Harvard, Matt returned to UWA, not in mathematics, but rather in the School of Public Health. He subsequently became Professor and has been deeply involved in the long-running Busselton Health Study with a particular interest in the epidemiology of cardiovascular and respiratory diseases. Moreover he works extensively in the evaluation of the effectiveness of programmes designed to promote physical activity.

The early 1980s also saw the appointment of Tony Pakes to succeed Richard Tweedie as the resident probabilist at UWA. He has contributed extensively to models of the evolution of the size of populations, particularly those subjected to immigration or emigration, and to the modelling of competition of fodder crops that propagate via seed banks. He has also studied topics in so-called extreme value theory; an example is the number of record attempts that are made in order to break some currently standing record mark.

Richard Tweedie had left UWA to become the Foundation Director of Siromath, a quantitative consulting company established by CSIRO. From 1983 to 1987 Siromath provided John Henstridge with experience in commercial statistical consulting. John had been a tutor at UWA for three years from 1976 and then spent four years as a biometrician with the UWA School of Agriculture. In 1988 he established his own consulting company, Data Analysis Australia, which is based in Perth and has steadily grown to become Australia's largest and most successful strategic data consultancy. It now has over 20 staff and services the needs of government, commerce and industry throughout Australia. John devotes much time and effort towards professional accreditation by the Statistical Society of Australia (SSA) of working statisticians, and his company supports generously the activities of the Young Statisticians Group of the SSA as well as the Western Australia Junior Olympiad. He is currently President of the SSA.

Following academic positions both in the UK and Australia, and after a period as Director of the University of Melbourne Statistical Consulting Centre, Tim Brown was appointed to the Chair in Statistics at UWA in 1987. His research was devoted mainly to the approximation random processes with applications telecommunication networks. Tim's rich experience in consulting helped to further secure the UWA Statistical Consulting Group. While consulting with the Ford Motor Company, he became a convert to the Total Quality Management movement. At UWA, Tim introduced a third-year unit on industrial statistics, possibly the first in Australia, and put much effort into writing mathematics texts for the new Year 12 secondary curricula. He left UWA in 1992 to become the Chair of Statistics at the University of Melbourne and subsequently served as Dean of Science at ANU and the pro-Vice-Chancellor for Research at Latrobe University.

Ross Maller left a Principal Research Scientist position with CSIRO to join UWA Mathematics in 1989 and was appointed the Professor of Quantitative Finance in the Business School 10 years later. Ross was an experienced consultant and his interactions with agronomists at the CSIRO led to collaboration with Tony Pakes and a joint research monograph. During the 1980s Ross worked

closely with investigators in the UWA Crime Research Centre constructing novel models of 'criminal careers' with the objective of predicting patterns of recidivism, particularly in relation to sex crime. Ross moved to ANU in 2003, where he is now an ARC Professorial Fellow.

Other significant appointments in statistics in the 1990s include those of Peter Taylor, Adrian Baddeley and Murray Aitkin. Peter was only at UWA for a short time (1990–1901) but contributed substantially to modelling queuing and telecommunication networks by determining structures that yield tractable representations of long-term distributions (for example, the length of a queue). Peter took his skills to the Telecommunication Research Centre at the University of Adelaide and later was appointed (Australia's first) Professor of Operations Research at the University of Melbourne. Murray spent three years at UWA as a Australian Research Council Senior Fellow while on leave from the University of Newcastle (UK).

Adrian arrived at UWA in 1994 with an already formidable reputation for his work in stochastic geometry, spatial statistics, stereology and quantitative microscopy. His research at UWA enhanced further his international standing as attested by his election to the Australian Academy of Science in 2000, receipt of its Hannan medal in 2001 and the awards in 1995 of the Medal of the Australian Mathematical Society and the 2004 Pitman Medal by the SSA. Adrian's work runs the gamut of deep theoretical insight, analysis of spatially varying data and the writing of a very high-quality software package for analysing spatial data. Key themes of his results include the extension of known statistical methodology to spatial data thereby furnishing means by which the degree of accuracy of an idealised model compared to real data may be determined. Adrian has written several definitive reviews of progress in his areas of interest.

Luchezar Stoyanov, a pure mathematician, worked in the area of analysis, geometry and topology, focusing on difficult questions about Hamiltonian dynamics, geodesic and billiard flows, and spectral and scattering theory. As well as his UWA PhD students, Lucho's collaborators included the distinguished international experts V M Petkov and F Takens.

During the 1980s, links were forged between pure mathematicians and logicians in the UWA departments of Mathematics and Philosophy who convened a joint study group to read books and papers on topics such as the nature of proof and different kinds of logic. Among the participants was Graham Priest who published his book In Contradiction just prior to taking up a Chair in Philosophy at the University of Queensland in 1988. Alan Woods continued the work in logic. He was interested in the connections of logic and computational complexity within algebra, combinatorics and number theory. Alan's name is attached to the Erdős-Woods numbers; these are integers k such that between some two values n and n+kevery number has a factor in common with either n or n+k. The smallest of these numbers is k=16, discovered by Alan, associated with the interval [2184,2200]. It is now known that there are in fact infinitely many Erdős-Woods numbers and the first few dozen of them are listed in the on-line encyclopaedia of integer sequences.

Links were also forged between mathematicians and

engineering. From the mid-1980s Lyle Noakes studied applications of differential geometry in mechanical engineering, robotics, control theory and approximation theory, with international collaborations at IBM Research, EPFL Lausanne and Imperial College, London. Contributions were also made by PhD students in mathematics, in electrical engineering, and in computer science at UWA, and by UWA staff in mathematics, computer science and political science. Another link between mathematics and engineering was a long-running collaboration between Mike Alder, Chris deSilva and their PhD students on applications of geometry and linguistics in pattern recognition.

Notable among the pure mathematicians in this period was Simon Fitzpatrick, a UWA alumnus, who returned as lecturer to UWA in 1982 after a period in the US. Not only was he respected for his contributions to mathematics through his work on analysis, he also earned the award of International Correspondence Master in 1999 by the International Correspondence Chess Federation based in Switzerland, and was captain of the Australian correspondence chess team in the CC Olympiad XIV preliminaries, the chess-equivalent of the Olympics and conducted by email.

INTO THE 21st CENTURY

Although it might be argued that mathematical advances arising from Western Australia had been dominated by results from applied mathematics and statistics, the 21st century has seen a dramatic shift of emphasis with workers in pure mathematics achieving some remarkable breakthroughs. The reason for this success can be attributed largely to the vision and drive of Cheryl Praeger the foundation Director of the Centre for the Mathematics of Symmetry and Computation (CMSC) housed at UWA. In 2006 she was awarded an Australian Research Council (ARC) Professorial Fellowship and also became the first Australian-based mathematician to be invited to serve on the Executive Committee of the International Mathematical Union. In 2007 she became the first pure mathematician to win a prestigious ARC Federation Fellowship and in recent years the outstanding CMSC has developed tremendously. This Centre has attracted a healthy number of strong researchers as international visitors, postgraduate students and externally funded postdoctoral researchers. Its external visibility is greatly helped by the maintenance of a mathematical blog (SymOmega, http://symomega.wordpress.com/) by three of the members of the CMSC.

Cheryl's research focus is primarily with aspects of mathematical symmetry and how certain mathematical structures (known as groups) act on structures that possess symmetry. The exploitation of this symmetry enables impossibly difficult problems to be made tractable. She has developed classification methods that can be used to study large networks like the internet. Other prominent mathematicians in UWA with similar interests include Cai-Heng Li and Michael Giudici. Cai-Heng has proved a number of quite stunning results about the symmetry of large networks, including solutions to several issues that have been open questions for many decades. Moreover, we believe that Cai-Heng is the most highly cited mathematician currently in Western Australia and was

promoted to Professor in June 2013. Michael is currently the Deputy Director of the CMSC and the author of a book on the detailed structure of finite classical groups. Another strand of interest within CMSC is with various geometrical problems and this area has been significantly strengthened by the recruitment of two world-class mathematicians John Bamberg and Alice Devillers onto the permanent staff. The CMSC also attracted Akos Seress from Ohio State University but his time in the Centre was regrettably short due to terminal illness.

In Western Australia there is currently much activity in the general area of combinatorics, which is concerned with the study of finite or countable discrete structures. Gordon Royle, the current CSMC Director, transferred to the Mathematics Department at UWA from Computer Science and is renowned for his monograph on Algebraic Graph Theory. He maintains a website containing catalogues of combinatorial objects that is widely used by combinatorialists worldwide. Very recently he has been working on the mathematics of the puzzle Sudoku and in particular addressing questions such as: what is the fewest number of entries that need to be given in a Sudoku such that the problem has a unique solution? Other Western Australian combinatorialists include Lou Caccetta, Jamie Simpson and Amy Glen. Jamie, from Curtin, is interested in number theory and the combinatorics of finite sets; in particular he works with Amy at Murdoch on the combinatorics of words.

As well as pure mathematics research in WA, work continues in other areas of mathematical science. Martin Hazelton at UWA worked with Adrian Baddeley and one of their papers had the rare distinction of having been read to the Royal Statistical Society. Martin also conducted research involving the economics of motor traffic, for example estimating the trip rates from certain origin-destination data. He left UWA in 2005 to take up the Chair of Statistics at Massey University in New Zealand. The economic theme was continued by Jiti Gao who devised and applied nonlinear time series models to climatic and financial data. Jiti moved from UWA to a Chair in Econometrics at the University of Adelaide and recently moved to Monash University. The current Professor in Statistics at UWA, Berwin Turlach, researches in the area of computer-intensive statistical methods and its applications with particular results having relevance to biostatistics, hydrology and forensic science. Studies in applied mathematics have been strengthened immensely by the recent appointment of Michael Small from Hong Kong. To show that not all mathematicians pursue what many people think are very specialised and intrinsically dull subject matter, Michael wrote a paper in 2012 concerning how a computer can be used to give a gambler the edge over the casino when playing roulette. The paper, which appeared in the wellregarded Chaos, was the most highly read article published in the journal during the year.

AND THE NEXT FIFTY YEARS?

If there is one lesson to be learnt from the history of the development of the mathematical sciences, it is that it is seldom predictable. We have already alluded to the fact that our forerunners would probably be very surprised as to some subjects that are accepted as belonging in modern mathematics and statistics. With that in mind, to expend

too much effort in looking to the future serves little purpose. Nevertheless, there are some aspects of the present Western Australian scene that provide strong evidence of some of the mathematical work that will be required. The subject of operations research is likely to be of interest to many of the resource industries, especially those in remote locations for whom questions of efficient scheduling and allocation of personnel and equipment are important. Equally there are likely to be tremendous opportunities for those mathematicians and statisticians with skills in the area of the analysis and processing of data. We now know that a significant part of the Square Kilometre Array is to be located in rural Western Australia. This experiment is predicted to generate mind-boggling quantities of raw data that will need to be processed in an efficient way and devising procedures to do this is likely to represent a formidable intellectual challenge.

We can be confident that the immediate future of mathematical sciences in Western Australia is in safe hands. Recent appointments at the State's various universities have secured many young researchers who come with excellent records and very promising careers ahead of them. More worrying though is the longer-term fate of the mathematical sciences both locally and, more generally, nationally. There is a well-reported drop in the number of high-school students opting to study advanced year 12 mathematics courses and this does not augur well for the fate of the subject in the medium to long term. Perhaps the onus is on those presently working with mathematics—and this includes engineers, economists and physical scientists through to medical and agricultural scientists-to make it more widely known that advanced mathematics is not only important both for intrinsic interest and its multitude of highly relevant applications but, perhaps selfishly, can lead to exciting and fulfilling employment.

ACKNOWLEDGEMENTS

We thank all those who have provided input for this article including Walter Bloom, Alice Devillers, Peter Kloeden, Mark Lukas, Ute Mueller, Volker Rehbock and K L Teo. Tania Blackwell (UWA) is thanked for her technical support. We also are grateful to the referees for their comments that led to substantial improvements in the presentation of the manuscript.

REFERENCES

BHATHAL R 1999. Cheryl Praeger; mathematician in Profiles: Australian Women Scientists, pp. 143–151. National Library of Australia, Canberra.

BLAKERS L 1979. MAWA-an historical note. Sigma 100, 21-23.

COHEN G L 2006. Counting Australia in: the people, organisations and institutions of Australian mathematics. Halstead Press, Broadway Bay (in association with The Australian Mathematical Society).

FOWKES N & SILBERSTEIN J P O 1995. John Mahony 1929–1992. Historical Records of Australian Science 10, 265–291.

Gani J 2001. In memory of Larry Blakers (1917–1995). Australian Mathematical Society Gazette 28, 25–26.

Magain M 2011. Charlie Weatherburn and the flying machine. Self-published <charlieweatherburn.com>

Mahony J J 1968. Obituary Harris Charles Levey. Journal of the Australian Mathematical Society 8, 1–5.

Received 26 April 2013; accepted 17 July 2013

Editor's note

PUBLICATION DATES OF JOURNAL OF THE ROYAL SOCIETY OF WESTERN AUSTRALIA VOL. 96, 2013/14

The publication dates given on the cover of each issue of the journal are indicative rather than actual publication dates. The printed issues were published on the following dates:

96 (1) pp. 1–39

16 September 2013

96 (2) pp. 41-95

6 March 2014

REVIEWERS 2013

The Editor would like to thank the following people who reviewed manuscripts submitted to, or published in, the Journal of the Royal Society of Western Australia in 2013.

Mike Bamford
Hugo Bekle
Andrew Boulton
Don Bradshaw
Colin Branch
Ron Burman
Lindsay Collins
Mike Craig
Richard Davy
Russell Frew
John Glover
David Guest
Stuart Halse
Adrienne Hardham

Kathy Haskard
Roger Hocking
Steve Hopper
Barbara York Main
Harriet Mills
Mick O'Leary
Colin Pain
Tom Pinceel
Phil Playford
Terry Speed
Brian Timms
Kate Trinajstic
Malcolm Walter
Simon Wilde

[©] Royal Society of Western Australia 2014

JRNL N42-43

.

WA Science

Journal of the Royal Society of Western Australia

Instructions to Authors

WA Science publishes peer-reviewed articles dealing with research in all aspects of the natural and physical sciences of relevance to Western Australia. Research papers reporting original research should not normally exceed 5000 words; review papers should not exceed 10 000 words. Short papers/Research notes not exceeding 2000 words will be given priority in publication. Discussions and Replies of recently published papers in the journal should not exceed 1000 words.

Authors are encouraged to submit a list of potential reviewers in Australia or overseas, but choice of reviewers is at the discretion of the Editor. Submission of a paper is taken to mean that the results have not been published or are not being considered for publication elsewhere. Authors are solely responsible for the accuracy of all information in their papers, and for any opinions they express. Papers accepted for publication become copyright of the Royal Society of Western Australia, unless Crown Copyright in claimed, and the corresponding author will be required to assent to the transfer of copyright, signing of behalf of all co-authors in the case of multi-authored papers. A pdf of the published paper is provided free to corresponding authors and their coauthors; hard copy offprints may be ordered at proof stage at a rate of \$100 (incl. GST and postage) for 50 offprints.

Manuscripts should be submitted as pdfs or Word (doc or docx) files to the Editor in the following format: Title page; Abstract; Key words; Text; References; Figure captions; Tables; Appendices (if any); and Figures.

Headings: Authors may use up to four levels of headings, all of which are left justified: first-order headings are bold capitals; second-order headings are bold upper and lower case; third-order headings are capitals; and fourth- order headings are upper and lower case. All pages should be numbered consecutively, including those carrying tables and captions to figures.

Illustrations: All illustrations, both line drawings and photographs, are to be numbered as figures (not plates) in sequence, and each must be referred to in the text in consecutive order. In composite figures made up of several photographs or diagrams, each part should be designated by a lower-case letter (e.g. Figure 2b).

Authors are advised to use the most recent issues of the Journal as a guide to the general format and bibliographic style of the manuscript, and to conform as closely as possible to the style in preparing the manuscript. The metric system (Sl units) must be used. Taxonomic papers must follow the appropriate International Code of Nomenclature, and geological papers must adhere to the International Stratigraphic Guide. Spelling should follow the Concise Oxford Dictionary. Following the review process, authors should revise their manuscript and send one printed copy together with a digital (doc or docx) file to the Editor for final technical editing.

The Title should begin with a keyword.

The Abstract should not be an expanded title, but should include the main substance of the paper in a condensed form.

Six to ten Keywords should be provided.

The Text should be organised under the following headings: *Introduction*, which should contain the reasons for doing the work and essential background material, but not the results or conclusions; *Methods* (if applicable), which should provide sufficient details of techniques to allow them to be repeated; *Results*, which should not include material more appropriate to the discussion; *Discussion*, which should emphasise the significance of the results and place them in the context of related work; *Conclusions*, which summarise the main findings of the paper; *Acknowledgements*, which should acknowledge any appropriate assistance from colleagues and also the journal reviewers.

References must be set out as follows, with journal titles spelled out in full.

Paper:

BEVAN A W R, 2014. History and roles of the Royal Society of Western Australia. WA Science 97, 1-12.

Book:

HARPER J L 1977. Population biology of plants. Academic Press, London.

Chapter in Book:

Davie P J F & Short J W 1995. Decapod — Anomura, Brachyura. In: Wells F E, Hanley J R & Walker D I (eds) Marine biological survey of the southern Kimberley, Western Australia, pp. 118–126. Western Australian Museum, Perth.

High-quality Illustrations are required, no larger than 300 mm x 400 mm, with sans serif lettering suitable for reduction to appropriate publication size (81, 115 or 170 mm wide). Scale must be indicated on illustrations. Photographs must be good quality prints, not exceeding 170 mm x 252 mm. Colour figures incur a charge of \$300 (incl. GST) per colour page. Additional printing costs for folding maps and charts will be charged to authors: please consult the Editor before submitting these items. Figures should also be provided as high-resolution (300 dpi) tif, jpg or eps files to ensure high-quality reproduction.

Extensive sets of data, such as large Tables or Appendices, may be classed as Supplementary Papers and not printed with the paper but lodged with the Society's Library (held in the Western Australian Museum, 49 Kew Street, Welshpool, WA 6106). They should be supplied in printed and digital form (preferably as pdfs). Copies of a Supplementary Paper may be obtained from Society's Library upon payment of a fee.

Contributions should be sent to:
Editor-in-chief
WA Science
journal@rswa.org.au

Also available from the Royal Society of Western Australia:

(Prices are ex GST; discount prices for members are in parentheses)

Regular issues of the Journal (price per part)		\$12	(\$8)	
The Leeuwin Current: An Influence on the Coastal Climate and Marine Life of Western Australia (Volume 74, 1991)		\$20	(\$15)	
Plant Diseases in Ecosystems: Threats and Impacts in South-Western Australia (Volume 77, Part 4, 1994)		\$20	(\$15)	
De Laeter Symposium on Isotope Science (Volume 79 Part 1, 1996)		\$20	(\$15)	
Symposium on the Design of Reserves for Nature Conservation in South-western Australia (Volume 79, Part 4, 1996)		\$20	(\$15)	
Mini-symposium on Remote Sensing and its Applications in Western Australia (Volume 80, part 1, 1997)		±\$20	(\$15)	
Granite Outcrops Symposium (Volume 80, Part 3, 1997)	*	\$20	(\$15)	
Centennial Issue 1897-1997 (Volume 81, Part 1, 1998)		\$20	(\$15)	
Management of Granite Outcrops (Volume 83, Part 3, 2000)		\$20	(\$15)	
Leschenault Inlet Estuary (Volume 83, Part 4, 2000)		\$50	(\$35)	
Fire and Wetlands on the Swan Coastal Plain (Volume 88, Part 3, 2005)		\$20	(\$15)	
Holocene sedimentation, stratigraphy, biostratigraphy, and history of the Canning Coast, north-western Australia (Supplement to Volume 91 Part 1 2008)		\$25	(\$20)	
Leeuwin Current Symposium 2007 (Volume 92 Part 2, 2009)		\$65	(\$45)	
The Habitats of the Western Australian soldier crab <i>Mictyris occidentalis</i> Unno 2008 (Brachyura: Mictyridae) across its biogeographical range (Supplement to Volume 92 Part 3, 2009)		\$25	(\$20)	
Symposium on Evolutionary Biology (Volume 92 Part 4, 2009)		\$45	(\$35)	
Symposium on Kimberley Marine and Coastal Science (Volume 94 Part 2 2011)		\$65	(\$45)	

Please add postage and handling at the following rates:

	Australia	Overseas
Regular issue	\$5.00	\$6.00
Thematic Issues	\$6.00	\$10.00 (Surface Mail)
The Leeuwin Current: An Influence on the Coastal Climate and Marine Life of Western Australia	\$12.00	\$18.00 (Surface Mail)
DeLaeter Symposium on Isotope Science	\$12.00	\$18.00 (Surface Mail)
Granite Outcrops Symposium	\$12.00	\$18.00 (Surface Mail)
Leschenault Inlet Estuary	\$15.00	\$30.00 (Surface Mail)
Leeuwin Current Symposium 2007	\$12.00	\$20.00 (Surface Mail)
Kimberley Marine and Coastal Science Symposium 2011	\$12.00	\$32.00 (Surface Mail)

Combined postage discounts apply, airmail POA

Please send your order, including payment (all prices in Australian dollars), to: Honorary Treasurer, Royal Society of Western Australia, PO Box 7026, Karawara, Western Australia 6152.

WA Science © is published by: Royal Society of Western Australia, PO Box 7026, Karawara, Western Australia 6152 ⊠ rswa@museum.wa.gov.au

ISSN 0035-922X Print Post Approved PP642409/00008.

Claims for non-receipt of the Journal should be submitted within 12 months of publication, to: RSWA Librarian, PO Box 7026, Karawara, WA 6152

⊠ rswa@museum.wa.gov.au Address changes should be submitted to: Membership Secretary, PO Box 7026 Karawara WA 6152.

© ROYAL SOCIETY OF WESTERN AUSTRALIA 2014

This work is copyright. Apart from any use as permitted under the *Copyright Act 1968*, no part may be reproduced by any process without written permission from the Editor-in-chief of the Royal Society of Western Australia, ⊠ journal@rswa.org.au. A permissions line must be provided

crediting author(s) and WA Science – Journal of the Royal Society of Western Australia as the source.